ON THE COMPARATIVE OSTEOLOGY OF THE LIMPKIN (ARAMUS VOCIFERUS) AND ITS PLACE IN THE SYSTEM

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SIXTEEN FIGURES

In the world's avifauna there are two birds contained in the genus Aramus. They have the appearance of large rails, and, very much like these, they inhabit marshes and extensive swamps and bogs. One species—the Aramus scolopaceus of Gmelin—ranges through Brazil, Guiana, and Venezuela, while our United States species—A. vociferus—occurs in Florida, the Greater Antilles, Central America, northward to South Carolina, and, very rarely, westward into Texas.

A number of years ago I prepared an illustrated account of Aramus vociferus, comparing its skeleton with those of rails, cranes, and allied birds; but as no good opportunity offered at the time for its publication, the manuscript and figures were set aside with others I was at work upon then. Later on this material was taken up again, and I published a brief, illustrated synopsis of it, which, while useful in some ways, was quite inadequate for working avian osteologists.[1] In that contribution, however, there was presented the schemes of classification of the super-suborders Gruiformes and Ralliformes of a number of the most eminent avian taxonomists, of this and the last generation, as Merrem, Huxley, Garrod, Sclater, Newton, Reichenow, Fürbringer, Sharpe, Gadow, and others.

The crane-rail group at that time I considered to form the suborder Paludicolae, an opinion at variance with the one I now hold.[2]

[1] Shufeldt, R. W. on the osteology of certain cranes, rails, and their allies, with remarks upon their affinities. Jour. Anat. and Phys., Lond. October, 1894, vol. 29; N.S., vol. 9, pt. 1, art. 5, pp. 21–34; text figures.

[2] Shufeldt, R. W. An arrangement of the families and the higher groups of birds. Amer. Nat., vol. 37, nos. 455–456, November–December, 1904, pp. 833–857, figs. 1–6.

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There are three little tables given in the above cited article in the Journal of Anatomy, arranged in parallel columns. These tables present, in a comparative way, the salient osteological characters of Rallus longirostris, Aramus vociferus, and Grus americanus, and are very useful. Moreover, the article is illustrated by figures of the skull of the limpkin, a rail, and a crane, which, while they show the characters pretty well, are by no means as good as similar figures made by me of more recent dates. It is not my intention here to cite any of the numerous articles which have been published on the osteology of either the rails or the cranes and their allies, a number of which are from my own pen, contributed many years ago.

On the other hand, it is the specific object of this contribution to give a detailed account of the skeleton of Aramus vociferus, which is a chapter in avian osteology hitherto unpublished, and one which will prove to be highly useful to students of the subject in the future, particularly to paleontologists who may require such information at any time.

For many years the fact has been more or less generally recognized that Aramus is related to the cranes (Grus) on the one hand, and to the rails (Rallidae) on the other. This, however, is a question to be more thoroughly touched upon in the concluding remarks at the close of the present article. Further, it is fair to presume that many species of birds of past ages and eras have become extinct, which, were they in existence now, would not only fill in the above-mentioned gaps, but would render it at once clear exactly what the aforesaid relationships were among all these now most puzzling gruine and ralline genera and species of birds.

In so far as I am aware, none of the fossil cranes or rails discovered up to date have thrown much light upon this part of the subject, though there is no telling what future discoveries along such lines may have in store for us.

Unfortunately there are, at this writing, but few skeletons of the Gruidae at my disposal for examination and comparison; while among the Rallidae there are a larger number of species and genera of birds, both existing and extinct, which stand in

need of osteological description and comparison with Aramus, especially of the genera Rallus, Limnopardialis, Gymnocrex, Aramides, Aramidopsis, and other ralline groups, or birds supposed to be more or less nearly related to the typical forms we designate as rails.

Upon comparing the skeleton of such a species as Grus mexicana among the cranes or Gruidae with that of the limpkin, it would seem that the gap between these two genera and their affines upon either side is at least partially bridged over—that is, in so far as two representatives species can demonstrate it. Take the *skull* of Aramus for example. With equal truth one might say that it belonged to some bird that was either a rail-like crane or a crane-like rail; with such equality are the characters represented in it, that is, ralline and gruine ones. Especially is this true when we come to compare this skull with that part of the skeleton of Rallus longirostris crepitans on the one hand, and Grus mexicana on the other.

One of the most evident characters distinguishing it from Rallus is its having a pretty well marked supraoccipital prominence, with an occipital foramen upon either side of it; this is a gruine character. The vacuity in the interorbital septum is smaller than it is in either Grus or Rallus. Aramus has a short pterygoid, much dilated behind, and not seen in either the crane or the rail, where the pterygoids, although short, do not show this dilation. Its palatines and its laterally compressed, sharp-pointed vomer, with its inferior edge cultrate, are exactly what we find in Grus, this latter bone being more spreading in the clapper rail.

Its maxillo-palatines, being plate-like, are decidedly more gruine than they are ralline, as is also the broader interorbital frontal region above. The merest paring is taken off the edge of the superior orbital margins, to indicate the presence of the nasal glands, while those depressions are better marked in Grus, and still better in Rallus. In type the quadrates and lacrymals agree in all three of these genera. The broad orbital process of the first-mentioned bones are squarely truncated, exactly as we find them in Porzana. Aramus has its temporal fossae on the

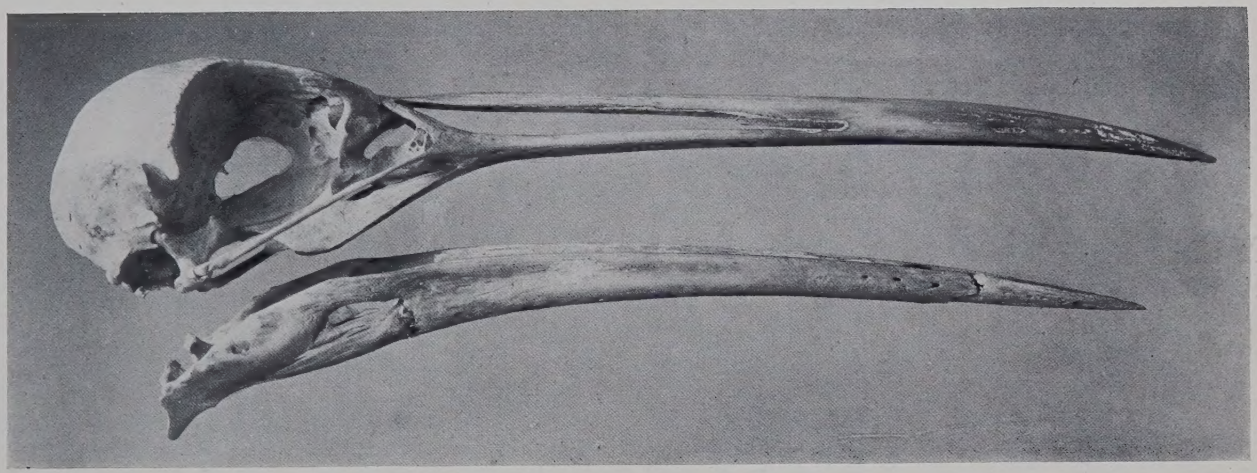


Fig. 1 Right lateral view of the skull of Aramus vociferus; natural size. Photograph by the author of specimen No. 19667, Collection U. S. National Museum; ♂ adult

lateral aspects of the skull concaved precisely as they are in Grus and Rallus, and all its supero-parietal region is beautifully rounded, as we likewise see it in the genera mentioned. Passing to the foramen magnum of Aramus, we find it to be quite circular in outline, while in Grus and Rallus it is cordate. Again, it differs from either in having the anterior wall of its brain-case thoroughly completed in bone, a feature, by the way, not often met with in birds. In its fronto-premaxillary region above Aramus exhibits the most perfect type of schizorhinalism, the sutures among the several bones there being very distinct, and remaining persistent during the life of the individual. The descending limbs of the nasals are antero-posteriorly broader than they are in either Rallus or Grus, while the nasal processes of the premaxillary—which extend from those bones and the palatine forwards—are more or less rounded and rod-like, not showing the supero-longitudinal grooving seen in the latter genus.

Pars plana is small and very distinct on either side, and lacks that elegant scroll-like process seen above and in front of it in Grus, in which it connects upon either side the lateral ethmoidal wing with the nether side of the fronto-nasal roof above. In all the birds thus far considered, the basitemporal region of the skull is, with respect to its characters, in very close agreement, and in them, too, the osseous aural entrance is very open, lacking the bony protecting walls so generously supplied by the squamosal and its neighboring bones in not a few other birds.

The long, acutely V-shaped *mandible* of Aramus, with its symphysis extending back for at least one-fourth its length, more nearly approaches the bone as seen in Rallus than the mandible in Grus. Its articular ends are abruptly truncated behind, and a good-sized ramal vacuity exists at the usual site upon either side. Borders or edges of either ramus above and below are rounded, as is also the under side of the mandibular symphysis, the upper part of the latter being longitudinally grooved. The hyoidean apparatus, the sclerotal plates of the eyeballs, and the ossiculae auditus require no special description.

In all the North American cranes and rails, including Aramus, the thyro-hyal rods seem to be the only part of the skeleton of the tongue that ossify, and the ring of bony platelets in an eye are all small for the size of any particular species to which they may belong.

Of the remainder of the axial skeleton: Between the skull and pelvis, Aramus has 23 vertebrae. With the possible exception of the *atlas* they are all thoroughly pneumatic, as in Grus. The postero-external angles of the neural arch of the first cervical are produced as processes, extending backwards, while the superior periphery of its cup is roundly notched out. In the *axis vertebra* we find a very low, tuberous neural spine, and a well-developed hypapophysial one. But what is unusual is that it has a good pair of parapophysial processes directed backwards. Its neural canal is small for the size of the bird. This is also the case in the third vertebra, after which this canal gradually enlarges, to become small again as it passes through the dorsal series, where it is of markedly small caliber, as it is in the pelvis. In the third vertebra the neural spine is very inconspicuous, likewise in the fourth, to be entirely absent in the fifth to the eleventh inclusive; whereupon, in the twelfth, it gradually begins to make its appearance once more, until it assumes the well developed quadrate plate seen in the dorsal vertebrae. In the third vertebra we see interzygapophysial bars connecting the pre- and post-zygapophyses, while in the fourth these are long and reduced to the most hairlike dimensions. The lateral vertebral canals also begin in the third vertebrae, and persist as such to the 16th cervical inclusive. Commencing, as I have said, in the *axis*, the narial parapophysial spines are present down the chain to include the *tenth*, they being very long and slender from the fifth. In the *eleventh* they suddenly disappear altogether, which is an interesting fact. From the fifth to the thirteenth cervical a hypapophysial open channel is developed for the passage of the carotid arteries; a small spine takes its place in the fourteenth vertebra. But this never becomes very large thereafter, and disappears entirely as we pass to the last four dorsal vertebrae. This hypapophysial

spine exhibits a tendency to trifurcate in the seventeenth segment of the column, but at the best it is but feebly accomplished. The 18th, 19th and 20th (dorsal) vertebrae are completely fused together, while the 21st, 22d and 23d are freely articulated. In these last three, long osseous metapophysial spines or ossified tendons of the spinal muscles ornament the neurapophyses and transverse processes, extending, as they do, both forwards and backwards. A slender pair of free ribs are suspended from the 17th vertebra; on the coössified 18th these connect with the sternum, as they do in the succeeding five dorsals. There is also a pair of pelvic ribs that meet the sternum by means of rather long hemapophyses. All these ribs are highly pneumatic, and the true thoracic ones have free unciform appendages upon their posterior borders. The second and third pairs of ribs are short and slightly stoutish, but they soon become, in the succeeding pairs, long, slender and narrow.

The *pelvis* of Aramus, in some important particulars, more closely resembles that bone in Grus than that in the Rallidae, though it is not lacking in the characters seen in the pelvis of the latter. Regarded upon superior view, we note that the faintly emarginated anterior ends of the ilia are squarely cut across, while the mesial margins of these bones rise up to fuse with the superior border of the sacrae crista, thus completely sealing in the 'neural canals' behind.

The surface of the preacetabular portion of either bone faces almost directly outwards. There are present no intervertebral foramina of the sacrum, such as we find in rails; and the postacetabular part of the pelvis, with the included sacrum, is bent downwards, so as to make a considerable angle with the fore part of the bone. Posteriorly, the ischio-iliac extremities extend far back of the last sacral vertebra, the posterior margin of the latter lying in the curve formed by the mesial edges of the ilia.

Viewed laterally, it will be seen that the external iliac borders of the postacetabular region extend over the outer aspects of the ischia, but, proportionally, not to the extent they do in some of the Rallidae, though rather more than in Grus. The planes in which the ischia are found are nearly parallel to each other,

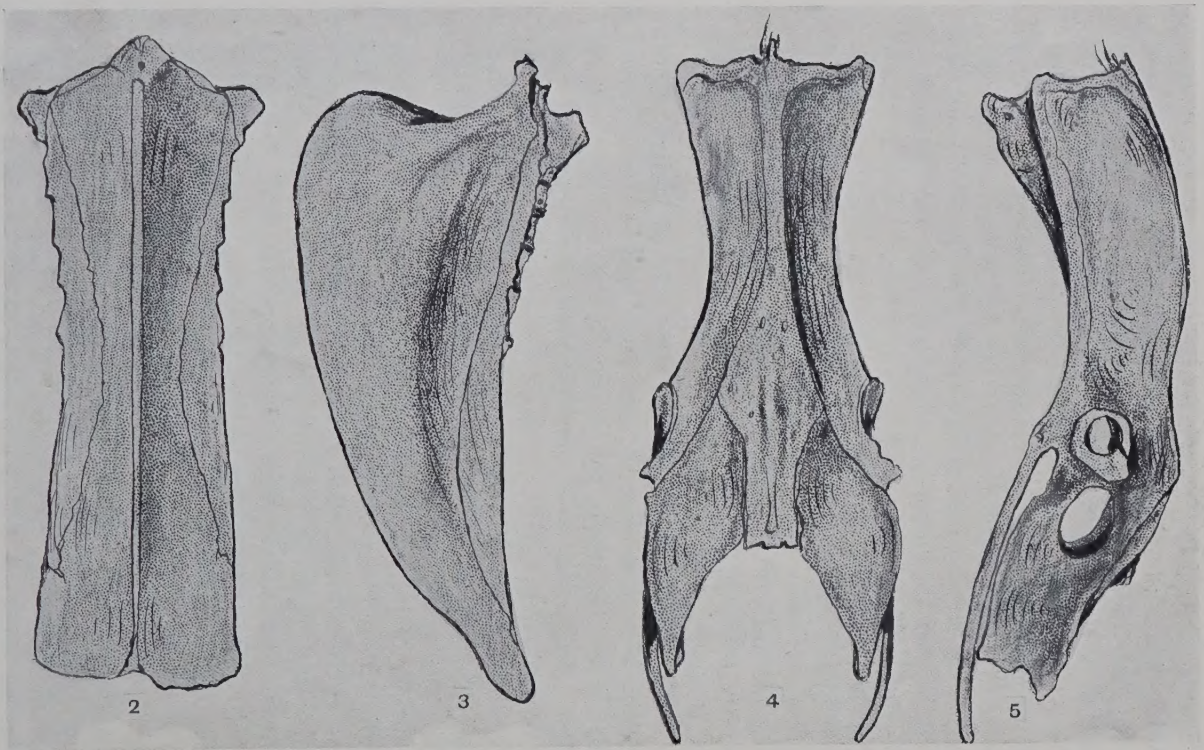


Fig. 2 Ventral view of the sternum of Aramus vociferus; adult; No. 11795, Collection U. S. National Museum.
Fig. 3 Same bone shown in figure 2, seen on left lateral view.
Fig. 4 Pelvis of Aramus vociferus; dorsal view; same specimen as before.
Fig. 5 Same bone as shown in figure 4, viewed on left lateral aspect. All specimens drawn natural size by the author.

and the ischiadic foramen is relatively small. The flat, rather broadish pubic style is separated by an open line coming in contact with the lower edge of the ischium above, and its distal extremity is produced well beyond the latter bone, to run out as it slightly curves towards the fellow of the opposite side. The posterior ilio-ischiadic margin exhibits hardly the semblance of a 'notch,' the edge of the former being in a line nearly perpendicular to the plane of the postacetabular region, or to the superior edge of the pubic style that extends beyond it. Seen upon ventral aspect, we find that the *five* leading sacral vertebrae throw out their lateral processes, to fuse with the ventral surface of the ilium upon either side; this agrees with Crex. In Grus, *seven* of the leading sacrals behave in this manner. In Aramus the next four vertebrae have their elevated diapophyses completely concealed upon this view by the much swollen sacral body. Then follow five more vertebrae, which have stout transverse processes thrown out as braces against the inner margins of the ilia. The first pair of these are the longest, and they rapidly graduate down to the ultimate sacral. In the case of the first pair, too, the outer ends of their transverse processes meet, upon either side, the superior periphery of a cotyloid ring, and posterior to this point they fuse with the outer ends of the diapophyses of the next vertebra behind. But these two only—the two true sacrals—are thus linked together. The renal fossae are deep and circumscribed, especially by the folding forwards of the postero-ventral parts of the ilia, as they do both in Grus and all typical Rallidae.

There appear to be *six* free *caudal vertebrae*, but they are small, and have all their outstanding processes considerably aborted. A sub-quadrilateral *pygostyle* of better proportions finishes off the distal extremity of the spinal column in this remarkable bird.

Passing to its *shoulder-girdle*, we find coracoids, scapulae, and os furcula all highly endowed with pneumaticity. The first-mentioned are rather short bones; antero-posteriorly compressed, and lacking an epicoracoidal process, but developing an elegant, forward-curling scapular wing (from the mesial side

of the shaft), which presents, well up, that foraminal perforation seen in the coracoids of several other groups of birds. A generous articular facet occupies the mesial two-thirds of the lower border of the expanded sternal part of either one of these coracoids, and this facet is grooved for its entire extent in the transverse direction. This groove admits of perfect articulation with the rounded transverse eminence occupying nearly the entire length of either coracoidal facet of the sternum. Disagreeing with both Grus, and the Rallidae, the coracoids of Aramus slightly decussate in their sternal beds.

Os furcula is a broad U, without a hypocleidium, and with its transversely flattened rami, of no mean width, extending, without narrowing in the least, to include the symphysis, the anterior and posterior plane surfaces of which latter have gradually come to face the other way. The free, upper clavicular ends are bluntly truncated, and support each an articular face, for a coracoid and scapula of the corresponding side.

A *scapula* is a rather short bone, elegantly curved outwards, drawn gradually to a point behind, and its outer blade decidedly flattened in the vertical direction. Its head is large, and is occupied, at their usual sites, by extensive facets for the os furcula, the coracoid, and the demi-facet of the glenoid cavity. At the under or ventral side of this end of the bone, just within the coracoidal facet, we always find a pneumatic foramen, which is very large in Grus.

The *sternum* of Aramus is very long and correspondingly narrow. Its carina is inclined to be shallow, and it extends the entire length of the sternal body, which latter is distinctly quadrilateral in outline, without any xiphoidal processes behind, but showing there a slight median emargination. The carinal angle is handsomely rounded off; the anterior carinal border above it is concaved and somewhat thickened; while the manubrial process is quite rudimentary. Either costal process is very much turned outwards, and is, comparatively, of no great height. The costal borders are transversely narrow; the haemapophysial facets upon them rather far apart, and their intervals occupied by deep little concavities. On the ventral aspect of the

sternal body, on either side of the keel, a strong, rough, muscular line is seen, extending nearly its entire length. It is uniformly concaved outwards, the surface of the bone being roughened within it and smooth without. The convexity of this 'pectoral line' is well separated by an interval from the base of the keel.

On the thoracic aspect of this sternum we find it deeply concaved in front, gradually shallowing as we pass posteriorly. A median line of small pneumatic foramina are seen, and others are found, upon this view of the bone, in various localities. Between the costal borders, where the thoracic concavity is deepest, the two sides of the sternal body are *flat*, and face each other at an open angle. In front, the anterior wall, which bears the coracoidal grooves upon its outer side, is deep and nearly vertically disposed.

Of the appendicular skeleton: Aside from the great difference in size, the *humerus* of Aramus is the very counterpart of that bone as we find it in Grus mexicana—even to the most trivial characters. In the former it has a length of 11 cm., just double that in the latter, and they differ from the humerus of the Rallidae in their being more completely pneumatic. The pneumatic foramen is a single hole, and the ulnar and radial crests are strongly developed; so is the thick humeral head, which is separated from the ulnar crest by a deep valley. The smooth shaft shows the double sigmoid curve and is subcylindrical on section. At the distal end we find the articular trochleae and of the usual form. There is a very rudimentary epicondylar process.

Having compared in detail the remaining bones of the pectoral limb of Aramus with the corresponding ones in Grus mexicana, I find them likewise, as in the case of the humerus, to agree, character for character, throughout, except in the matter of size. As a rule, the various bones have in Grus rather more than double the lengths of their counterparts in the antibrachium and pinion of Aramus. They are not pneumatic but inclined to be stoutish in proportions. An *ulna* is concavely bowed along its anconal border, while the palmar one shows a row of papillae for the quill-butts of the secondary wing feathers. The proximal end is, in proportion, larger than ordinary, as compared with the

distal extremity. This is so in order to support the articular cavities for the large trochleae of the humerus. An olecranon process is pretty well developed also. The radius is slightly bowed along its inferior border, and its carpal end is larger than its head. On the whole it exhibits the usual ornithic characters. This also applies to the two small bones of the wrist, and the various ones that make up the skeleton of the pinion. In the *carpo-metacarpus* the medius metacarpal is bowed and a trifle longer than the stouter and straight one of index. There is constantly present in both Grus and Aramus a minute hole on the anconal aspect of the head, between the tubercle that occurs there and the trochlear surface, which, inasmuch as it is not a pneumatic one, must be for the entrance of a nutrient vessel. The central portion of the expanded part of the proximal phalanx of index digit is very thin, and occasionally shows a single pin-hole perforation in the limpkin, but not in the crane, as a rule. Nothing peculiar is exhibited on the part of the terminal finger-joints, and pollex digit bears a claw.

None of the bones of the *pelvic limb* in either Aramus or Grus are pneumatic. In the majority of their essential characters, the corresponding ones in the two genera agree, except, of course, in the matter of size, thus being in Grus considerably longer and larger in every way. As to lengths, however, they differ in proportions, as will be seen from table 1, given in millimeters.

TABLE 1

	FEMUR	TIBIOTARSUS	TARSO-METATARSUS
Grus	129	314	185
Aramus	84	181	136
Differences	45	133	49

In other words, twice the length of the femur in Aramus would be 168 mm. against 129 mm.—the length of the femur in Grus mexicana—showing the bone to be considerably more than twice the length in the former, as compared with the length of that in the latter. Whereas, in the case of the tibiotarsus,

twice its length in Aramus would be 362 mm. against 314 mm. of the bone in Grus, showing it to be nearly double the length—as 39 mm. is to 48 mm., the differences as thus compared. The differences in the tarso-metatarsi are nearer what they are in the femora, as may be seen from the above table.

In Aramus the *femur* has a shaft that for its middle third is nearly cylindrical, the bone as a whole being slightly bowed in the anterior direction. Its great trochanter is very broad transversely, and its crest rises above the articular summit, being continued round on to the anterior aspect of the upper third of the shaft. A deep pit exists for the ligamentum teres on the semiglobular caput femoris. At the distal end the condylar portion is greatly developed; the rotular channel in front is very marked, as is its continuation below as the intercondyloid fossa. The inner projection of the external condyle is sharp and prominent, and the pits in the neighborhood for muscular and ligamentous attachment very distinct. The lowermost points of the condyles are nearly in the same horizontal plane, and the popliteal depression is not especially concaved. On the surface of the shaft we find the usual muscular lines well marked.

If Aramus and Grus possess *patellae,* they have been lost from all the material at present at my command, and at this writing I cannot speak with certainty upon that point.

The shaft of the *tibio-tarsus* is very straight, being flattened in front and rounded behind. Its pro- and ectocnemial crests are well developed, but they do not extend down on the shaft, the latter process being hooked with its plane at right angles to the former, which stands out about perpendicular to the surface of the anterior aspect of the shaft. The rotular crest is only very moderately developed. At the distal end of this bone we meet with the usual characters found there in all ordinary birds. For the confinement of some of the anterior tendons, we find the little osseous bridge spanning a deep groove, with the tubercles above it, one on either side, for the attachment of the ends of a ligament that fulfils a similar purpose. Of ordinary size, the condyles are separated by a well marked intercondyloid groove, it being especially so in front. The internal condyle

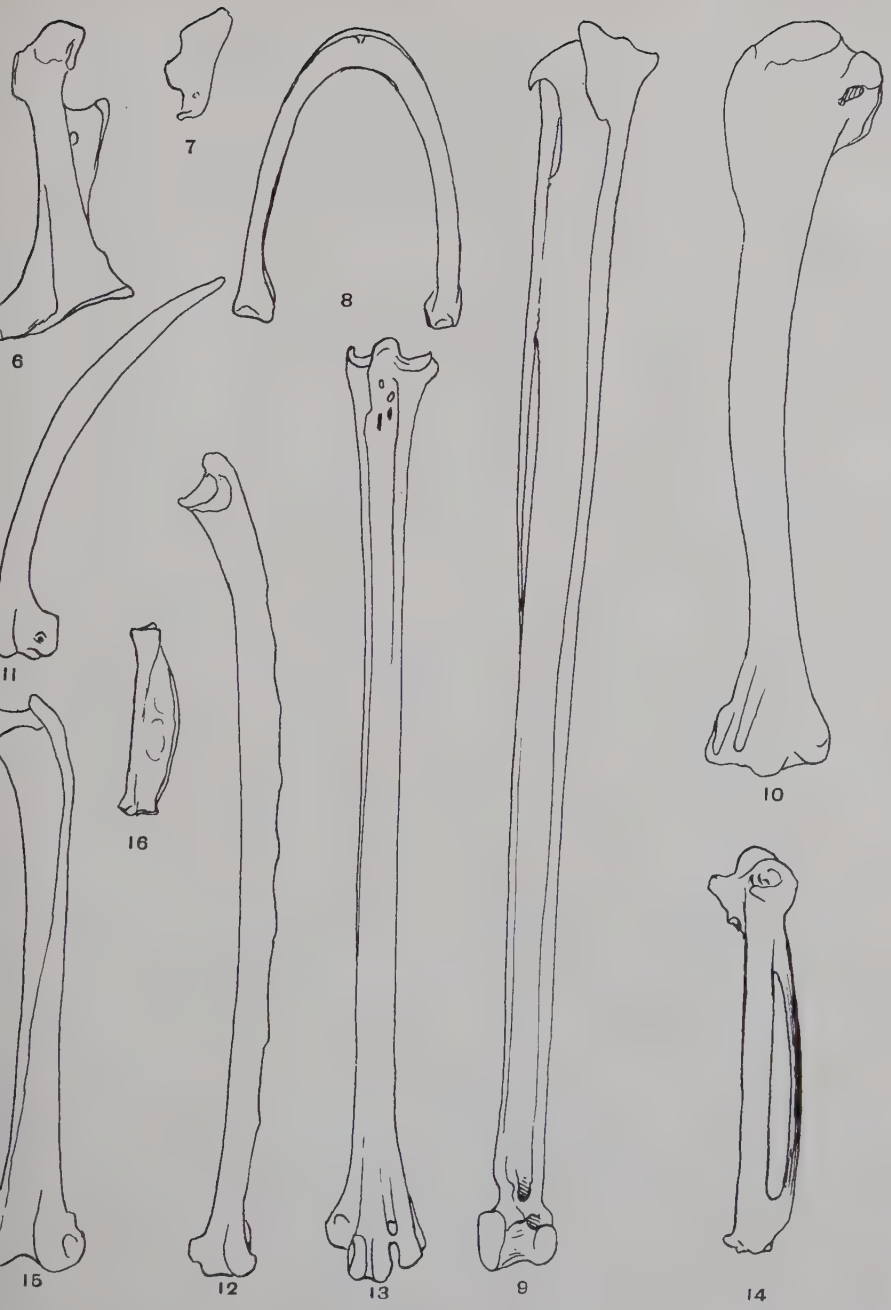
is sharp behind, where it projects; is shallow in the vertical direction, and long in the antero-posterior—this being less the case in the external one. Both have the usual reniform outline.

Aramus has an incomplete *fibula*, its lower extremity fusing indistinguishably with the outer side of the tibio-tarsal shaft at about its middle. The articular fibular ridge is high up on the latter, and has a length of about 2.5 cm.; fusion does not take place at this point. he head of this bone is rather large, transversely flattened, and produced backwards. On the outer side of the upper part of its shaft is a small, deep, spiral groove for the tendon of the *biceps flexor cruris* muscle.

Tarso-metatarsus has its shaft quite as straight as that of the tibia. Its sides are flat, but before and behind it is longitudinally grooved for the passage of tendons. In either case, this grooving extends the whole length of the bone, but is deepest on the anterior aspect for its upper third. On the summit of the bone the articular concavities are deep, and at the fore part between them the interarticular rounded prominence is conspicuous. The hypotarsus, though fairly well developed, is not especially so, and it is hardly at all extended down upon the back of the shaft. It has one main groove which is deep and nearly closed over posteriorly. Within, this groove is partially subdivided into two by a more subordinate median longitudinal crest. Upon either side of the hypotarsus we find a small perforating foramen. The anterior exits of these are close together just above the tubercle for the tendon of the tibialis anticus muscle in front. At the distal end of the shaft the trochlear processes are rather large and distinctly separated from each other. The lateral ones curve towards the median

Fig. 6–16 Various bones of the limpkin (Aramus vociferus); natural size. Drawn by the author in outline from specimen No. 11795, collection U. S. National Museum.

Fig. 6 Anterior aspect of right coracoid. Fig. 7 Coccyx, left surface. Fig. 8 Front view of os furcula. Fig. 9 Anterior aspect, right tibio-tarsus and fibula. Fig. 10 Anconal aspect, left humerus. Fig. 11 Right scapula, upper surface. Fig. 12 Left ulna. Fig. 13 Left tarso-metatarsus, from in front. Fig. 14 Left carpo-metacarpus. Fig. 15 Left femur, anterior surface. Fig. 16 Proximal phalanx, index digit.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plane behind, particularly the inner one of the two, which is at the same time the highest on the shaft. The next in this latter respect is the external one, the lowest on the shaft being the mid-trochlear process. Between this and the outer one is found the usual perforating foramen for the anterior tibial artery.

The small free *first metatarsal* is but slightly twisted upon itself (about half a turn), and presents nothing beyond what we usually see in that bone in birds; it has a length of 9 mm.

Aramus has the normal type of foot for birds, that is, 2, 3, 4, 5 joints to 1 to 4 toes respectively. As a rule the phalanges are long and slender, agreeing in this and other respects better with this part of the skeleton in Rallus than with Grus mexicana. Ungual joints are well developed and somewhat curved. All the sides of these latter are longitudinally marked by very distinct groovelets.

In both Aramus and Grus there is a great disposition for most of the tendons of the muscles of the pelvic limb below the thigh to ossify. In many cases they form stout, osseous rods, of very considerable length; others are beautifully dilated for half their lengths, like a small, partly opened fan, composed of the most delicate radii, being formed by that part of the tendon which is spread out in or on the muscle. In a disarticulated skeleton of Grus mexicana before me, there are between 60 and 70 of these ossified tendons, and about half that number in a similarly prepared skeleton from a specimen of Aramus.

From this description it will be seen that this rail-like bird belongs in a different family from the Rallidae—that is, in the family Aramidae, as pointed out by me in my classification of Aves, published in The American Naturalist in 1904 (vol. 38, nos. 455–456, Nov.–Dec., p. 852), which stands thus:

Supersuborder	XIII	RALLIFORMES
Suborder	XX	Fulicariae
Superfamily	I	Heliornithoidea
Family	I	Heliornithidae
Superfamily	II	Ralloidea
Family	I	Rallidae
	II	Aramidae

THE PARAPHYSIS AND PINEAL REGION OF THE GARTER SNAKE

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FORTY-ONE FIGURES

The pineal region of the vertebrates has been studied by a large number of investigators whose interest has been directed especially to the parietal organ and epiphysis, the significance and functions of which are still so problematical. On account of the relatively high state of development of the parietal organ in Sphenodon and many lizards, the reptiles have received special attention and the papers of Warren ('11) on the development of the pineal region in the lizard and turtle, Dendy ('99) on Sphenodon, and Voeltzkow ('03) on the crocodilian furnish rather complete pictures of the development of the region in each one of these groups. The snakes have received very little attention from this point of view and are only very imperfectly known. It was for the purpose of filling up certain serious gaps in our knowledge regarding this group that the present study was undertaken.

The literature dealing with the pineal region in snakes is very restricted. The earliest reference to this region is Hoffmann's ('85). In describing briefly the pineal region in Tropidonotus natrix, he called attention to a thickening of the roof of the brain at the boundary between the telencephalon and diencephalon. He offered no suggestion as to its significance but there can be little doubt that it was the anlage of the paraphysis which he saw. Hanitsch ('88) in a paper which I have not been able to see for myself, describes according to Leydig ('97) an organ which he supposed to be a well defined parietal eye in an embryo Vipera berus. He described the eye as provided with a lens in

which were pigment masses. Leydig thinks that Hanitsch was in error regarding this structure, and in his own investigations on Coronella he found nothing comparable to a parietal eye. In the stage described by Leydig, the paraphysis is characterized by the presence of many budlike evaginations and the epiphysis has become solid though it still retains its connection with the roof of the diencephalon by means of a hollow stalk penetrating the posterior commissure. Studnicka ('93) studied the epiphysis and paraphysis of an advanced embryo and a full-grown specimen of Tropidonotus and found the epiphysis to consist of a massive, ellipsoid body connected with the roof of the diencephalon by a thin stalk. The epiphysis itself was of a glandular structure. It was divided into lobes by connective tissue septa and exhibited a small cavity at the junction of the stalk and the body proper. In the adult form the same condition was found except that the cavity was wanting. Sorensen ('94) figured a sagittal section of the diencephalon of an embryo black snake in which the epiphysis was connected by an attenuated stalk with the roof of the diencephalon and was inclined caudad. He also figured a cross-section of the epiphysis of the garter snake which was a globular body. The failure of these investigators to find a parietal organ is probably because of the advanced age of the embryos studied and the temporary occurrence of that organ. The most complete account of the development of the pineal region in the snakes is that of Ssobolew ('97) on Tropidonotus and Vipera. In the former the epiphysis is described as a double evagination of the cerebral vesicle at the point of division between the di- and mesencephalon. The lumen of the epiphysis is still in wide open communication with the brain when the paraphysis first appears, and at its distal end exhibits "eine kleine Vertiefung mit der Bildung von zwei rundlichen Körnern,—dem vorderen und hinteren." The former he interprets as the anlage of the parietal organ, the latter as that of the epiphysis. At this stage the wall separating the two does not quite reach the level of the wall of the diencephalic roof. Ssobolew's figures fail to show the parietal organ so that a clear picture of the relationship of this organ to the epiphysis is still

lacking. In view of my own findings in Thamnophis and the irregularities which appear in the epiphysis, there may still be some question as to the exactness of his interpretation. In Vipera he described, without a figure, the anlage of the parietal organ as an anterior evagination from the epiphysis resting directly on the anterior epiphysial wall and accordingly elevated through the growth of the latter while not itself growing materially. All trace of the parietal organ disappeared later in both snakes. So far as I have been able to find, these are the only papers devoted to the development of the epiphysis and parietal organ in the snakes, although several have described the condition in the adult animal, for instance, Rabl-Rückhardt's ('94).

For a full account of the literature on this subject reference should be made to Studnicka ('05) and Gaupp ('98).

The observations upon which this study is based were made upon a series of some 20 embryos of Thamnophis radix, the ordinary garter snake, ranging in length from about 10 to 100 mm. The lengths of the younger specimens could be obtained only approximately on account of their being coiled in a tight spiral. These embryos were projected and drawn by means of a camera at a magnification that was exactly determined in each case and was about 10 diameters; the length was then scaled off on the drawing by means of dividers. In the stages in which the cerebral flexures were marked, the most prominent point of the mesencephalon was regarded as the most anterior point. The older embryos were sufficiently flexible to permit a straightening of the coils and direct measuring. These embryos I have grouped into five stages for convenience of description. Stage I is characterized by its $2\frac{1}{2}$ spirals and length of 11 mm. The choroidal fissure of the eye is invisible from the exterior; the mandibular, second, and third visceral arches are evident. The otocyst from the lateral aspect has a simple triangular form. In Stage II the olfactory pits have become constricted to form small nostrils. The body length is 18 mm. and there are $3\frac{1}{2}$ coils. Stage III has an approximate length of 30 mm. In Stage IV the length is about 42 mm. and the number of coils is $4\frac{1}{2}$ or 5. The phalli are well developed and everted at this time in the

males. Stage V has a length of 80 to 100 mm. and is characterized by the disappearance of the mesencephalic flexure of the brain.

The roof of the forebrain included in the present study comprises the following parts enumerated from posterior to anterior:

(a) The posterior commissure, occupying the roof of the synencephalon (or pars intercalaris of Burckhardt),

(b) The epiphysis or pineal body arising as an evagination immediately anterior to the posterior commissure,

(c) The superior commissure or commissura habenularis which connects the two ganglia habenulae, and which is situated immediately cephalad to the stalk of the epiphysis,

(d) The parietal organ or pineal eye situated in front of the epiphysis but separated later from it in the garter snake by the superior commissure,

(e) The postvelar arch (or dorsal sac of Goronowitsch or Zirbelpolster of Burckhardt),

(f) The choroid plexuses of the third and the lateral ventricles, arising from the roof of the anterior portion of the postvelar arch and sides of the telencephalon medium respectively,

(g) The velum transversum projecting into the encephalic cavity and separating the paraphysis from the postvelar arch,

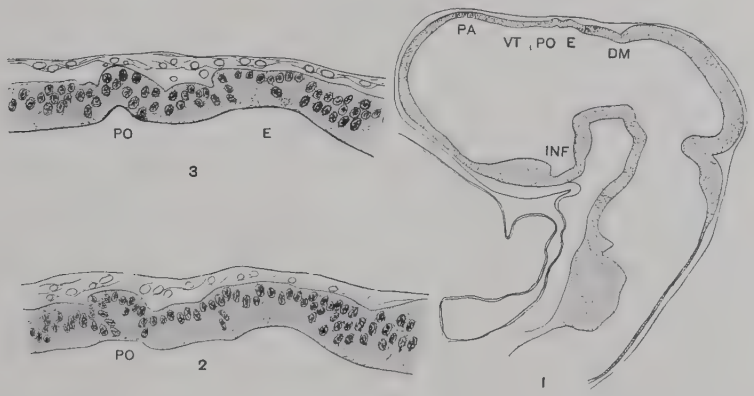
(h) The paraphysis, a median diverticulum from the roof of the telencephalon medium.

Stage I

At this stage the roof of the diencephalon exhibits two minute, inconspicuous evaginations separated from each other by a short interval (fig. 1). The anterior one of the pair, I believe, represents the anlage of the parietal organ, the posterior one, the epiphysis. The posterior one of the two is broader at its base than the anterior one, but both are of the same height and are inclined slightly so that the front wall of each makes somewhat less than a right angle with the roof of the diencephalon and the posterior wall rather more than a right angle. The anterior evagination is much compressed so that the lumen is very small,

ABBREVIATIONS

ACC, process from the roof of the diencephalon marking the attachment of the accessory parietal organ.
ACP, accessory paraphysis
BV, blood vessel
CH, cerebral hemisphere
DCP, diencephalic choroid plexus
DI, diocoel
DM, di-mesencephalic groove
E, epiphysis
FM, foramen of Monro
INF, infundibulum
LCP, lateral choroid plexus
P, paraphysis
PA, paraphysal arch
PC, posterior commissure
PO, parietal organ
SC, superior commissure
TM, telencephalon medium
TP, tuberculum posterius
TT, torus transversus
VT, velum transversum



Figs. 1–3 Sagittal sections of an embryo (C2) having a length of 11 mm. Stage I. Figure 1 is a combination of two adjacent sections through the brain, showing the relation of the epiphysis, parietal organ, velum, paraphysal arch, postvelar arch, and di-mesencephalic groove. × 20. Figures 2 and 3 are detailed drawings of the sections of the epiphysis and parietal organ from which figure 1 was made. × 230.

the posterior one opens by a wide mouth into the roof of the diencephalon. The distal ends of the two evaginations come in contact with the overlying external epithelium of the head. The velum transversum is present as a low ridge on the dorsal wall which continues laterally and ventrally and becomes more prominent at the sides than on the middle line and extends downward to the postoptic prominence. Externally ridgethis is manifest as a shallow groove.

The paraphysis is not visible at this stage. The paraphysal arch is simply a low, broad dome extending cephalad from the velum and passing over without interruption into the lamina terminalis as Tandler and Kantor have shown in their Stage II of Gecko. The position of the recessus neuroporicus is indicated by a space anterior to the paraphysal arch in which the encephalic wall is only about one-half as thick as it is immediately dorsal and ventral to it and where the basement membrane of the epithelium has disappeared and the space between it and the external epithelium of the embryo is filled up with a mass of polyhedral cells among which are many blood cells. The postvelar arch is very low. The diencephalon is separated sharply from the mesencephalon by a deep groove externally and a slight ridge internally.

The histological structure of the roof of the diencephalon exhibits several noteworthy features. In the postvelar arch there are two or three layers of nuclei situated toward the outer side of the brain. The preparations did not allow the outlines of the cells to be seen so that it is still a question how many layers of cells are represented by these nuclei. In the evaginations of the epiphysis and parietal organ the wall is only about two-thirds as thick as the rest of the postvelar arch and apparently is only one layer of cells in thickness. In the interval between the two evaginations the wall is thin, as in the evaginations themselves. The thickness of the roof behind these evaginations becomes gradually and uniformly thicker toward the di-mesencephalic groove; but the roof of the mesencephalon becomes suddenly nearly twice as thick as the thickest part of the diencephalic roof. In the evaginations the nuclei lie rather toward the outer ends of the cells. The front wall of both evaginations appear somewhat thinner than the posterior one, as Tandler and Kantor have observed in Gecko.

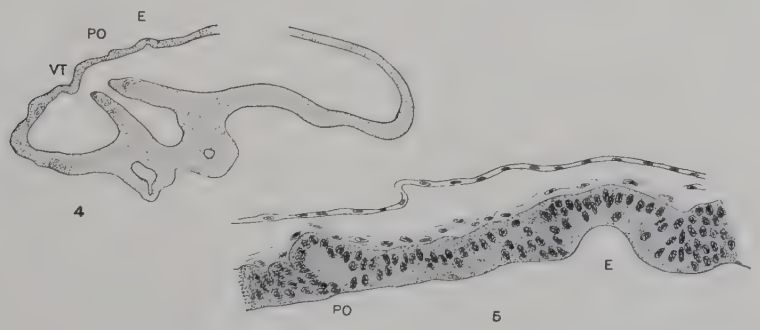
The line of demarcation between the anterior parencephalic and the posterior synencephalic portions of the diencephalon is marked by the epiphysis which arises from the extreme posterior end of the former region. The anlage of the posterior commissure is characterized at this stage by a zone of cells in the roof

of the synencephalon in which the cytoplasm is less dense than elsewhere. At this stage no traces of the other commissures of this region are visible.

The lateral and ventral prolongation of the velum transversum exhibits on its posterior aspect a very pronounced thickening having the form of a ridge that extends posteriorly and ventrally to the infundibulum. This ridge is very evidently anterior to the di-mesencephalic ridge which marks the division between the diencephalon and mesencephalon.

Stage II

This stage exhibits several slight advances over the preceding one in the region of the diencephalon. The epiphysis opens widely into the diocoel and is bowl-shaped, the cavity having a depth about equal to its antero-posterior diameter (fig. 5). The parietal organ has the form of a solid outgrowth from the roof of the diencephalon. Its cells are elongated and placed perpendicular to the surface so that it has the appearance of having been originally an evagination, as in the preceding stage, which has suffered a compression obliterating the lumen. In this



Figs. 4–5 Sagittal sections through the brain of an embryo (A2) Stage II, having a length of 18 mm., showing the parietal organ apparently constricted from the roof of the diencephalon so that its lumen is obliterated. The epiphysis is further removed from the parietal organ than in the embryo previously described. × 25. Figure 5 shows the epiphysis and parietal organ of the same embryo. × 230.

embryo the axis of the epiphysis is perpendicular to the roof of the diencephalon but that of the parietal organ is inclined forward as before.

The histological structure of the epiphysis is very different from that of the surrounding portions of the encephalic wall. The cells composing it are arranged in a single layer with the nuclei toward the outer ends of the cells. The wall of the parietal organ is not as thick as that of the epiphysis, but like the latter organ, its walls are of a single layer of cells with their nuclei toward their bases. The cytoplasm of these cells differs slightly from that of the epiphyseal cells in being more dense.

The velum transversum is visible as a slight ridge in the cavity of the brain and as a corresponding groove on the exterior. The paraphysis is just visible as a slight outpocketing of the apex of the paraphysal arch. Immediately dorsal to it is a large blood vessel. The cells composing it have a less dense cytoplasm than those forming the brain generally. The posterior commissure is quite clearly differentiated and the very slight constriction between the parencephalon and synencephalon is clear.

In another embryo of essentially the same size as the one just described, the paraphysis is apparently more highly developed. It has the form of a fingerlike evagination which is directed posteriorly. Its length is somewhat less than that of the epiphysis. Its posterior wall exhibits several wrinkles, as Ssobolew described in his Vipera embryo number 4. In this embryo I cannot be sure of the presence of a parietal organ. The plane of the sections (parallel to the roof of the synencephalon) was not favorable for the display of such an outgrowth, but a careful study of the series revealed nothing that could be interpreted as a parietal organ. The epiphysis has become somewhat larger than in the previous embryo described in this stage and slants distinctly backwards.

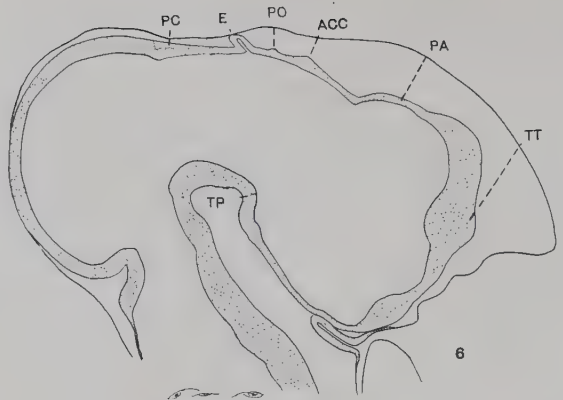
The telencephalon exhibits the two hemispheres and the telencephalon medium which is posterior and dorsal to the foramina of Monro. The paraphysis projects from the roof of this as a fingerlike evagination or, as in another embryo, as two very small evaginations. The telencephalon medium is greatly

compressed laterally and its sides are parallel so that the velum transversum is very narrow. It projects very slightly into the ventricle.

The posterior commissure in this stage seems very distinctly to lie in the second diencephalic segment of the brain and not in the mesencephalon as it has been usually described. It is situated a short distance caudad to the epiphysis. Thamnophis agrees in this regard completely with Lacerta and Chrysemys as described by Warren. In its earliest manifestation in the reptiles, the posterior commissure is wholly diencephalic. As will be shown later, however, it apparently encroaches upon the mesencephalon.

Stage III

The changes that have taken place in the pineal region at this stage are slight, but nevertheless perfectly evident. The epiphysis has increased in length so that it is now about twice as long as wide, and its axis inclines dorsally and posteriorly. Its cells are arranged in several layers and the posterior wall continues to be thicker than the anterior one and is slightly wrinkled. In one section the posterior wall bears a small budlike projection (fig. 11) the proximal half of the slender lumen is larger than the distal half although at the apex itself it is again slightly larger so that in sagittal section it looks almost as if it were divided into a cephalic and caudal branch. The apex of the epiphysis lies in contact with the external epithelium of the head and is surrounded by numerous large blood sinuses in the mesenchyme. In another embryo having a length of 33 mm. the epiphysis communicates with the ventricle of the diencephalon by a constricted neck (figs. 12 and 17). The parietal organ shows an appreciable advance in development over that of the earliest stage observed where it consists of a budlike outgrowth in wide open communication with the diencephalon on the middle line a short distance in front of the epiphysis. In this stage, as in the one immediately preceding, it has become solid, apparently by a pinching together in an antero-posterior direction. It has increased somewhat in



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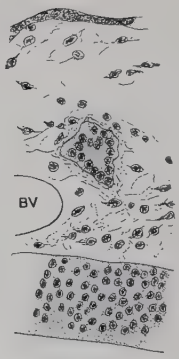

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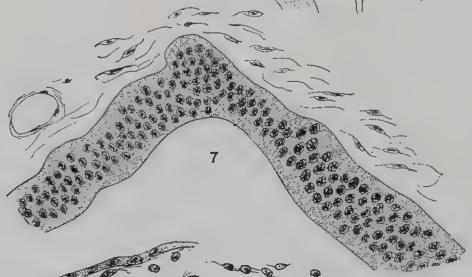

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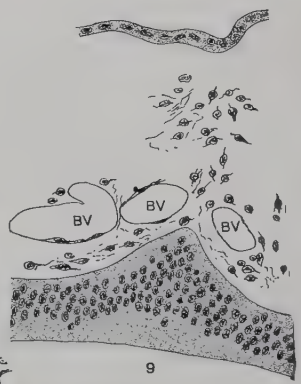

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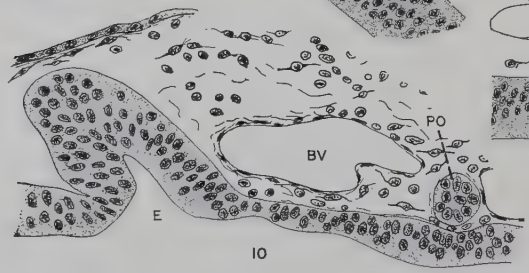

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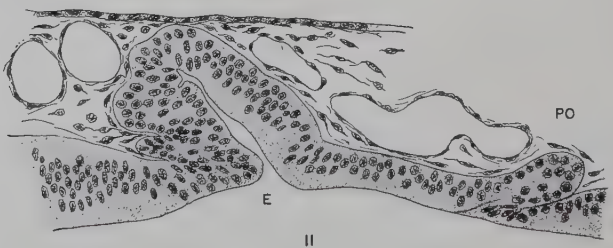

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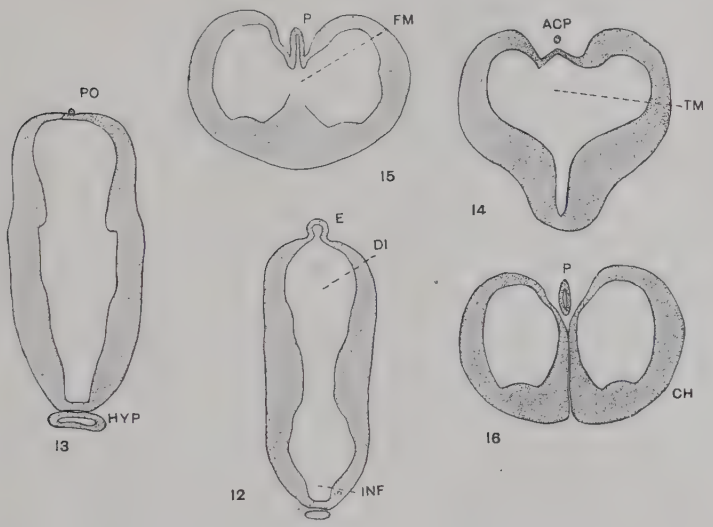


Figs 6–11 Sagittal sections of an embryo (J) having a length of 29 mm. Stage III. Figure 6 is a section through the entire head to show the general topography of the roof of the diencephalon. The section does not pass exactly through the paraphysis. × 20. Figure 7 is a detailed drawing to show the histology of the paraphysis which in this specimen was very slightly developed. × 230. Figure 8 shows the accessory parietal organ situated to the left of the mesial plane. × 230. Figure 9, the roof of the diencephalon on the mesial line at the level of the accessory parietal organ. × 230. Figures 10–11, adjacent sections through the epiphysis and parietal organ. The epiphysis is directed posteriorly; the parietal organ is suffering a lateral constriction from the roof of the diencephalon but is still in continuity with it; the epiphyseal wall has become much thicker than in Stage II. × 230.

Figs. 12–16 Transverse sections through an embryo (G) having a length of 33 mm. Stage III. × 25. Figure 12 is a section passing through the epiphysis and showing it slightly constricted off from the roof of the diencephalon. Figure 13 is a section 105 μ in front of the preceding and passing through the parietal organ. Figure 14 passes through the posterior portion of the accessory paraphysis derived from the roof of the telencephalon medium. Figure 15 shows the paraphysis cut through its attachment to the telencephalon. Figure 16 passes through the middle portion of the paraphysis.

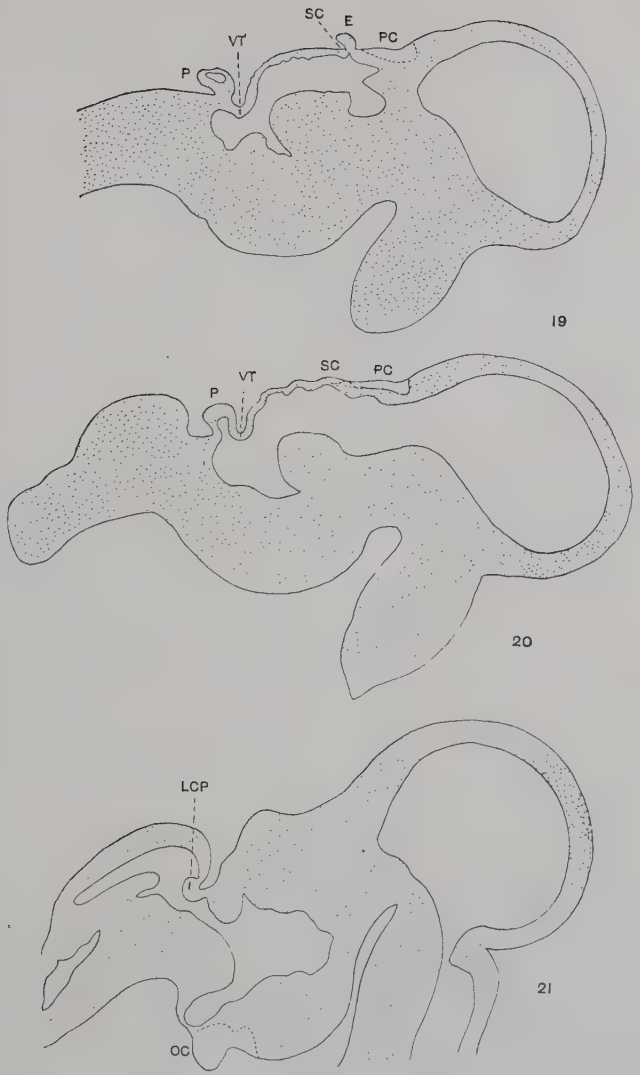
length and inclines cephalad so that its anterior face is for the most part in contact with the roof of the diencephalon in front of it. The portion of the roof of the diencephalon between the two evaginations continues to be made up of a single layer of

Figs 17–18 Portions of figures 12 and 13 respectively, to show the histological structure of the epiphysis and parietal organ. × 230.

cells. The parietal organ is made up of a single layer of cells in which the nuclei lie toward the basement membrane. In one embryo of this stage I could find no trace of a parietal organ.

At some distance in front of the parietal organ—about midway between the epiphysis and the velum transversum—the roof of the diencephalon exhibits a curious structure (fig. 9) whose significance may still be somewhat doubtful. Partly by an increase in the number of cell layers and partly by the increased length of the innermost layer whose clear cytoplasmic portion is relatively taller than elsewhere, the roof thickens to form a conical projection of small size. Separated by a short distance from the thickening mentioned there is a tiny nodule of cells lying in the mesenchyme similar in staining qualities to the roof of the brain (fig. 8). It lies 0.06 mm. to the left of the apex of the thickening but at such a level that its ventral limb is on a level with it. There is very distinctly a complete separation between the two structures but at the same time their form and position leave little room for doubt as to their earlier continuity. This evidently is an unusual structure for in my whole series of embryos it appeared only once. For the present it may perhaps be looked upon as an accessory parietal organ.

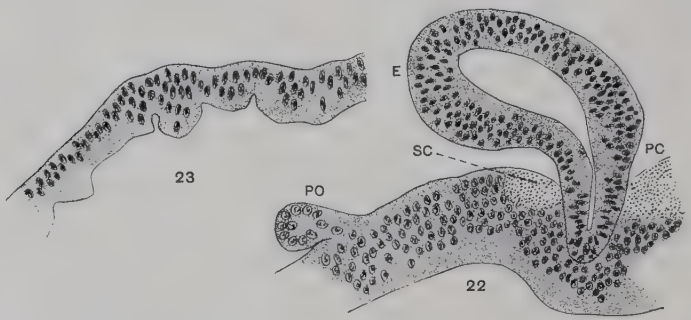
The velum transversum is in the form of a broad fold of the roof and sides of the brain projecting into the ventricles. The anterior and posterior limbs of the fold make an obtuse angle with each other. The anterior limb bears two very slight budlike evaginations which may become involved in the anlage of the paraphysis. In Lacerta muralis embryos 23. and 4.5 mm. long.



Figs. 19–21 Sagittal sections through the brain of an embryo (D2) 35 mm. in length. Stage III. × 20. Figure 19 shows the relation of the paraphysis and velum transversum and the earliest trace of the diencephalic choroid plexus. Figure 20 passes 45 μ to the right of figure 19, to show the connection of the paraphysis and telencephalon medium. Figure 21 shows especially the prominence formed by the ganglion habenulae and the development of the choroid plexus of the lateral ventricle.

Warren has shown three similar evaginations which he regards as the anlage of the paraphysis.

The paraphysis in an embryo having a length of 33 mm. consists of a triangular pocket which is very much compressed from side to side and which opens into the ventricle of the telencephalon medium by an opening greatly extended anteriorly and posteriorly. In another embryo of slightly greater length, 33 mm., the paraphysis extended as a fingerlike pouch somewhat compressed laterally and extending forward between the two cerebral hemispheres (fig. 16). The roof of the telencephalon medium



Figs 22–23 Sections of the same embryo as figures 19 to 21. × 230. Figure 22 shows the parietal organ in continuity with the roof of the diencephalon in front of the superior commissure. Figure 23 shows the anlage of the diencephalic choroid plexus.

slants laterally from the middle line at a low angle which increases to a right angle immediately behind the origin of the paraphysis.

In one of the specimens of this stage there is a small outgrowth behind the paraphysis, but in front of the velum transversum which resembles closely the organ described in another embryo of this stage as an accessory parietal organ (fig. 8). It has the form of a solid bud only 30 μ in diameter which is slightly constricted from the roof by a groove on its posterior side. Figure 14 shows a section immediately posterior to its connection with the roof of the brain. It may become involved in the paraphysis later, but the paraphysis is so well advanced in this stage

that it hardly seems likely. On the other hand it can scarcely be regarded as an accessory parietal organ since it originates from a segment of the brain anterior to the diencephalon.

The posterior commissure at this stage is clearly outlined. It does not lie immediately behind the epiphysis as at first, but is separated by a short portion of the roof, in this respect resembling Lacerta and Chrysemys as described by Warren. Later this portion of the roof of the synencephalon between the commissure and epiphysis becomes invaded by transverse fibers. In one embryo of this stage the transverse fibers seem to extend very slightly behind the groove separating diencephalon and mesencephalon.

Stage IV

At this stage the development of the pineal region exhibits considerable variation. Although the various specimens appeared externally to be of the same age, the relative development of the parts of this region varied greatly.

The posterior commissure has extended both caudad and cephalad, so that it reaches the stalk of the epiphysis in front and passes beyond the di-mesencephalic groove behind and occupies the entire roof of the synencephalon. Its fibers are very clearly differentiated by this time.

The epiphysis has still a simple form, being cylindrical or club-shaped, showing a differentiation into body and stalk. In two cases there was a wide open connection between the lumen of the epiphysis and the ventricle of the diencephalon; but in two other instances the pinching off seemed to be complete. The wall of the stalk is thinner than that of the body and in several instances the anterior wall is slightly thinner than the posterior one. Generally the body and stalk make an obtuse angle with each other, but in one case the stalk itself is bent. In one embryo in which the cavity of the epiphysis was completely severed from that of the diencephalon, a large blood vessel presses obliquely into the anterior wall (fig. 25).

The superior commissure can be distinguished as a small band of transverse fibers immediately cephalad of the stalk of the epi-

physis in the three embryos of this stage in which the epiphysis is still in communication with the diocoel, but in the other specimens which are more advanced in regard to the epiphysis, no trace of a superior commissure could be seen (fig. 28).

As might be expected, the parietal organ exhibits the greatest diversity of development. In one instance it was simply a solid budlike evagination as has been noted already in several of the earlier stages (fig. 22). In a second instance it was in the form of a solid pyriform mass of cells with the smaller end reaching almost to the roof of the diencephalon but not coming in contact with it (fig. 24). The axis of the organ in this embryo is inclined upward and forward at an angle of about forty-five degrees with the roof. The stem is a single column of cuboidal cells, the body itself exhibits a single layer of spherical nuclei around the margin with only a few situated internally. It has no trace of a lumen. It is notable in this embryo that the roof of the diencephalon is made up of only a single layer of tall columnar cells in the region from which the parietal organ apparently has separated whereas in the other specimens of this stage there are distinctly several layers. In a third embryo, the parietal organ has separated completely from the roof of the diencephalon and is in the form of a solid ovoid mass of cells with its long axis extending forward and upward. There was no trace of a lumen or stalk in this case (fig. 26). The roof of the diencephalon, however, was characterized by a slight irregularity in which the nuclei were rather crowded and squeezed toward the outer side of the roof,

Figs. 24–28 Sagittal sections of the roof of the diencephalon of three different embryos of 42 mm. length (Embryos B, R, and S). Stage IV. Figure 24 shows the parietal organ as a pyriform outgrowth separated from the roof of the diencephalon. × 230. Figure 25 is from the same embryo as the preceding and shows the lumen of the epiphysis closed off from the diocoel and a large blood vessel entering the anterior wall of the epiphysis. × 230. Figure 26 shows the parietal organ completely separated from the roof of the diencephalon in the form of a solid ovoid mass of cells and the epiphysis in open communication with the diocoel. × 230. Figure 27 shows the general relation of the parts of the brain of the same embryo as the preceding. × 20. Figure 28 shows the lumen of the epiphysis completely cut off from the diocoel and limited to the body of that organ, and the parietal organ as a hollow sphere of cells completely separated from the brain. × 230.

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indicating probably a very recent separation. Several blood vessels were in close relation to the organ. Still a fourth condition of the parietal organ was met with in another embryo in which it was in the form of a hollow spherical vesicle (fig. 28). It was in this instance made up of a single layer of cells and was completely removed from the roof of the diencephalon. The postvelar arch is large and domelike in this stage and is characterized especially by the numerous small wrinkles especially in its anterior portion (figs. 19 and 20). The anterior and posterior limbs make approximately a right angle with each other but the posterior limb is much longer than the anterior one. The velum transversum is well differentiated, with its two faces making an angle of about thirty degrees with each other. The epithelium of the front wall in the middle line is conspicuously thicker than that of the posterior wall.

The paraphysis has the form of an irregular conical or oval evagination in open connection with the cavity of the telencephalon medium. Usually it is slightly constricted at the base. It is considerably more voluminous than the epiphysis and its walls are more irregular. At this stage the blood vessels surrounding the paraphysis are very conspicuous.

The choroid plexuses exhibit at this stage marked advance in development over that of previous stages. The diencephalic plexus apparently appears later than the telencephalic, for at this time it is evident only as several bud-like thickenings of the postvelar arch projecting into the ventricle of the brain, and separated from each other by fairly deep clefts (fig. 23). The telencephalic plexus consists of an outgrowth extending anteriorly into the lateral ventricle from the wall immediately dorsal and lateral to the foramen of Monro (fig. 21). It is rounded at its free anterior margin and contains a large blood vessel. The histological differentiation of the telencephalic plexus is marked. The cells which are arranged in a single layer are more slender and taller than in the paraphysis and the cytoplasm is denser, and their nuclei are more elongated.

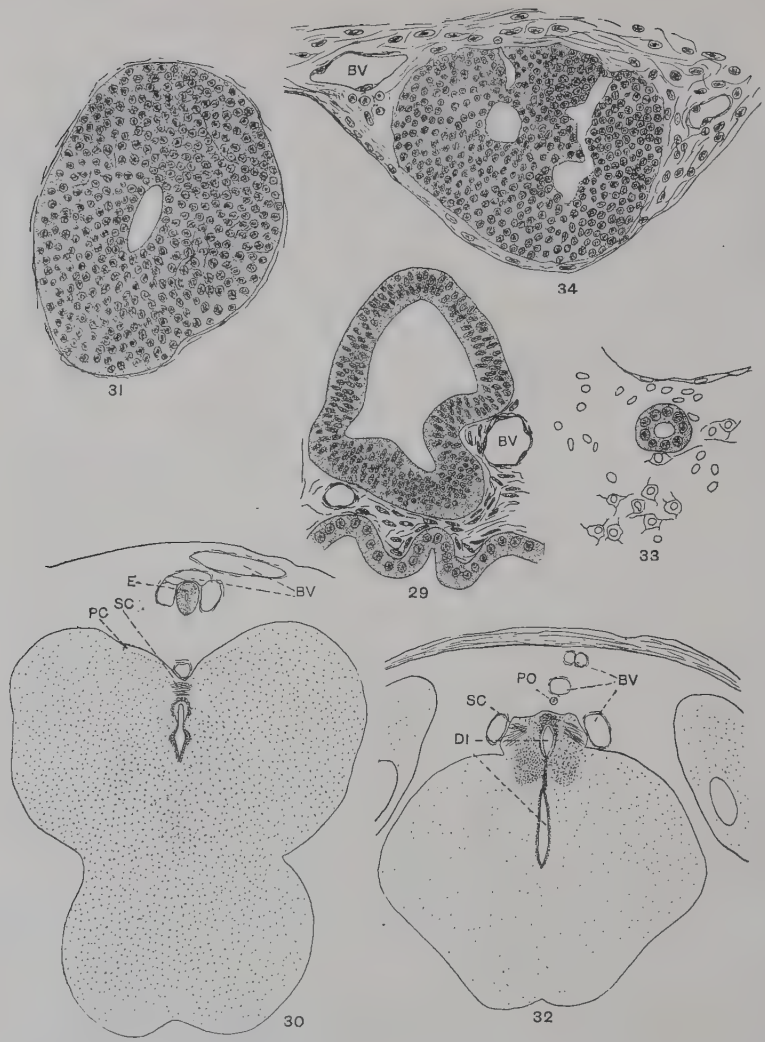
Stage V

The paraphysis at this stage has become much longer and has a horizontal position, its blind end pointing caudad (fig. 39), the choroid plexus of the lateral and the third ventricles are much folded and the epiphysis has become greatly elongated and its stalk has become solid.

The paraphysis extends from the roof of the median telencephalic ventricle at first dorsally and then turns at a right angle so that its distal half is horizontal. Its lumen is of somewhat irregular form. Proximally it is T-shaped, distally it becomes flattened dorso-ventrally. It lies in contact with the postvelar arch causing a distinct depression along the median line. The opening of the paraphysis into the ventricle of the telencephalon medium is exactly at the level of the opening of the foramina of Monro so that the ventricle widens quite suddenly immediately ventral to the opening of the paraphysis.

The velum transversum is difficult to delimit accurately. Its cephalic wall passes directly into the paraphysis and its caudal wall into the choroid plexus of the diencephalon. It is rather narrow from side to side, and at its sides it is very short. Medially it exhibits a longitudinal groove with parallel sides so that in cross-section it appears like a bilobed tongue depending from the dorsal wall of the brain. In general the velum has a vertical position. Its caudal surface bears several large oval or irregular prolongations which represent the choroid plexus of the diencephalon. These processes are not to be distinguished from those which hang down from the postvelar arch. They are in fact continuous with them.

The choroid plexuses of the telencephalon and diencephalon at this stage are quite complex in form. The latter has already been mentioned as made up of a number of irregular masses or folds from the caudal wall of the velum and roof of the diencephalon. It extends caudad as far as the level of the parietal organ and almost completely fills up the dorsal portion of the third ventricle which is nearly circular in cross-section. A study of the transverse series of sections of this region showed so

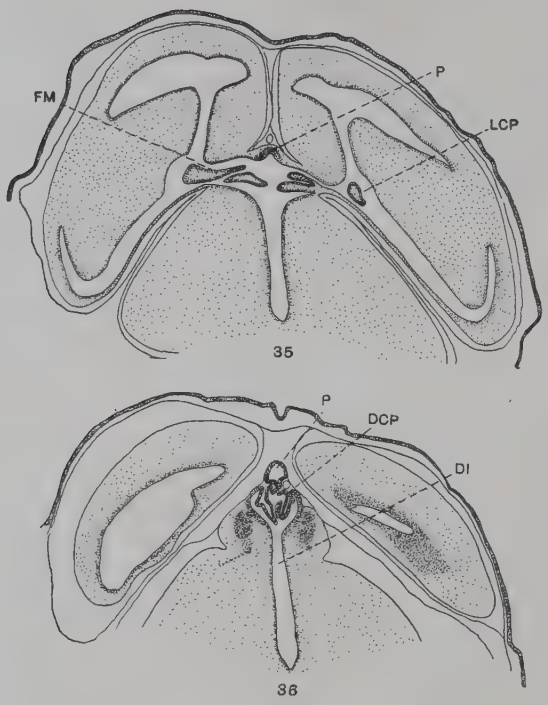


Figs. 29–34 Transverse sections through the brain of two embryos (D and C) having a length of 80 and 90 mm. respectively. Stage V. Figure 29 represents a section through the paraphysis of embryo D. × 230. Figure 30 passes through the epiphysis and the superior and posterior commissures of embryo C. × 20. Figure 31 represents a portion of the previous figure to show the histological structure of the epiphysis. × 230. Figure 32 is a section through the same embryo as the preceding but further anterior, passing through the parietal organ, ganglia habenulae, and superior commissure. × 20. Figure 33 shows the histological structure of the parietal organ of the same embryo. × 230. Figure 34 shows the histological structure of the epiphysis of embryo C, showing several clefts within. × 230.

great irregularity on the two sides that there can be no definite arrangement of parts. The telencephalic plexuses are likewise complicated. That of the lateral ventricle has the form of a plate of nearly horizontal position with its distal, lateral margin much thickened and turned up dorsally so that it has a concave upper surface. This plate extends anteriorly from the posterior side of the foramen of Monro so that the latter is partially obliterated by it. Warren describes the choroid plexus lateralis as springing from the paraphysal arch immediately in front of and lateral to the mouth of the paraphysis, invaginating the dorsomesial wall of the hemispheres. The plexus extends medially from its connection with the margin of the foramen of Monro so that it projects freely into the ventricle of the telencephalon medium and unites with the lateral wall of this ventricle by a slender stalk, ventral and lateral to the origin of the paraphysis (fig. 35). This median prolongation of the lateral plexus represents probably the telencephalic choroid plexus of Warren or the choroid plexus inferioris. It is wanting, according to Warren, in Lacerta but in Chrysemys there are described two paired masses growing back from the origin of the lateral plexus into the diencephalon. In Thamnophis they are confined to the unpaired ventricle of the telencephalon and do not extend posterior to the velum. The telencephalic plexus of the Amphibia, in which group it is most highly developed, arises from the paraphysal arch in front of the paraphysis. Warren thinks that these paired masses in Chrysemys may be the homolog of the amphibian telencephalic plexus.

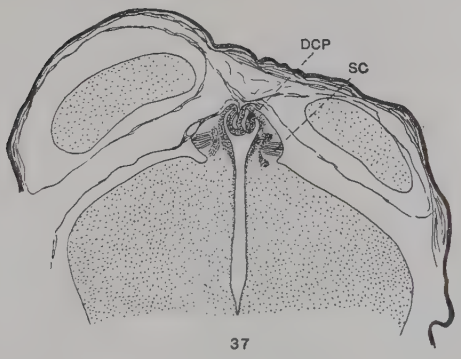
The parietal organ is present in an embryo having a length of 90 mm. as a hollow, ovoid body entirely separated from the roof of the third ventricle (figs. 32–33). Its long axis extends antero-posteriorly. It is situated about 50μ dorsal to the diencephalon, slightly nearer the stalk of the epiphysis than the distal end of the paraphysis (fig. 39). It is composed of a single layer of cuboidal cells with large spherical nuclei. A large blood vessel lies immediately dorsal to it.

The stalk of the epiphysis is very slender and has attained a considerable length. It passes into the roof of the diencephalon



Figs. 35–38 Transverse sections through the dorsal portion of an embryo (D), having a length of 80 mm., arranged from anterior to posterior, showing the paraphysis, lateral, median, and diencephalic choroid plexuses, ganglia habenulae, superior commissure, and a pocket of the roof of the diencephalon cut off by the superior commissure. × 20.

between the superior and posterior commissures and is directed almost exactly dorso-ventrally. The body of the epiphysis is large and pear-shaped. In one specimen it exhibited a small lumen in the anterior and ventral portion near its connection with the stalk, as has already been described in the adult serpent by Studnicka ('93). Its histological structure has changed markedly for now it is made up of an irregular mass of cells packed closely together with occasional connective tissue fibers. In another specimen there were several irregular clefts instead of a single lumen (fig. 34).



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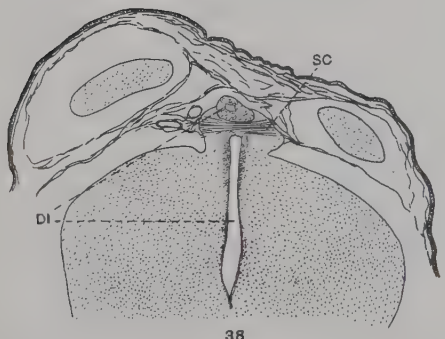

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The posterior commissure has increased much in size and occupies the entire roof of the third ventricle from the very attenuated stalk of the epiphysis posteriorly to the anterior portion of the mesencephalon. The superior commissure is strongly developed, forming a distinct projection from the roof of the diencephalon (fig. 32). The fibers of the superior commissure are much longer than those of the posterior and curve forward toward their ends, presenting thereby a concavity in front.

The diencephalon is very much compressed laterally. Anteriorly in the immediate region of the velum its sides are parallel, but further caudad it becomes widened in its dorsal portion around the choroid plexus so that it becomes nearly circular in cross section. Immediately ventral to the widened portion of

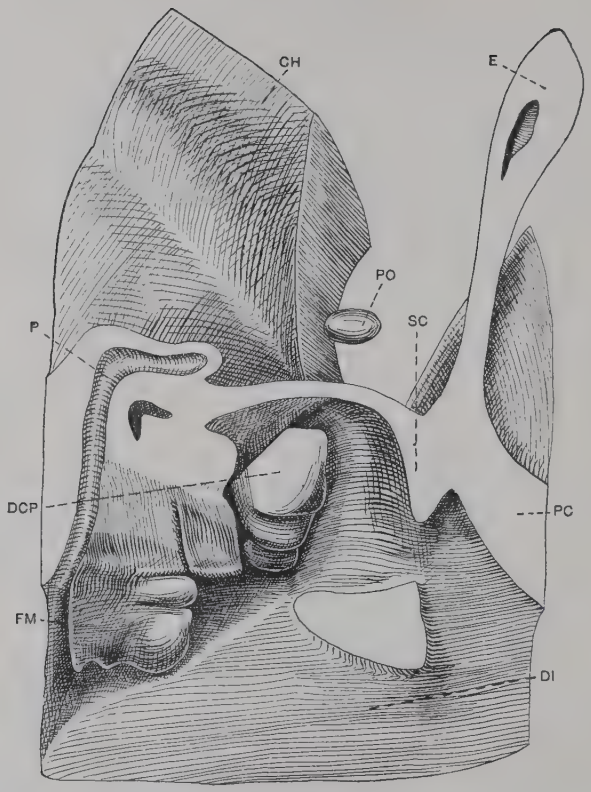

Fig. 39 Reconstruction of the pineal region of an embryo (C) having a length of 90 mm. Stage V. The right half of the model is viewed from the middle line. × 36.

the ventricle it becomes greatly narrowed by the development of the optic thalami until the space between the two walls is obliterated. The ependyma at the line of fusion becomes flat and indistinguishable except as a layer of cells which appear like fibers in cross-section. Dorsal to this line of fusion and extending caudad to it, in the region caudad to the superior commissure, the ependymal cells become very different from elsewhere, increasing greatly in height. These taller cells pass over directly into the cuboidal cells of the stalk of the epiphysis (fig. 40).

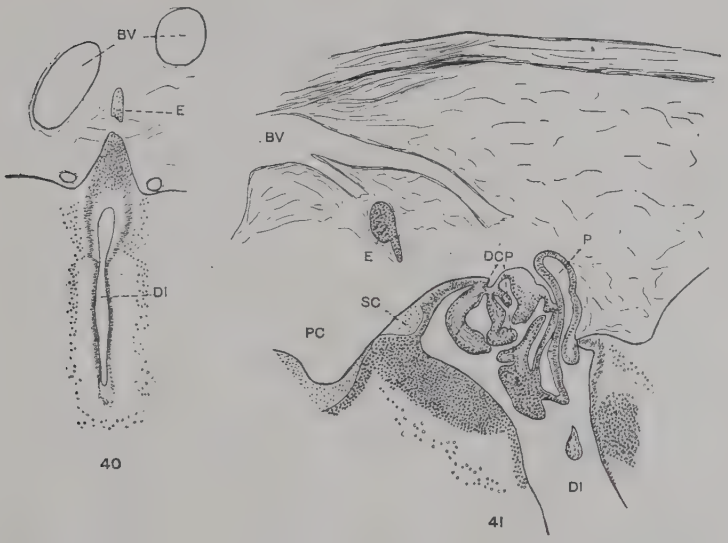

Fig. 40 Represents a transverse section through the stalk of the epiphysis of an embryo having a length of 90 mm. The section was accidentally broken across the stalk. × 50.

Fig. 41 Represents a sagittal section through the pineal region of an embryo having a length of 100 mm., showing the large blood vessel dorsal to the epiphysis. × 50.

Each ganglion habenulae forms a dorsal projection on the diencephalon in the region of the posterior end of the paraphysis. These two ganglia are separated dorsally by the much folded roof of the diencephalon making up the choroid plexus of the third ventricle. In one specimen the superior commissure apparently cuts off a portion of the roof of the diencephalon between the two ganglia so that there is a short pocket formed extending posteriorly above the commissure (fig. 38).

DISCUSSION

The present study on the development of the parietal region in the garter snake has thrown light upon several matters which have been the subject of much debate.

First of all, there can be little doubt left regarding the presence of a parietal organ in certain stages of the ophidians. Either

the organ described in this paper is the parietal organ or it is an organ entirely different from anything else described in the vertebrates. In favor of the interpretation here placed upon it, there may be mentioned; first, the method of origin as an evagination from the roof of the diencephalon anterior to the epiphysis and posterior to the postvelar arch; second, its form when at its maximum development; namely, a hollow spheroid consisting of a single layer of cells. Against this interpretation may be mentioned; first, the appearance of the parietal organ later than the epiphysis; second, its wide separation from the epiphysis with the superior commissure separating the two; and third, its failure to migrate dorsally to lie in close proximity to the dorsal side of the head. The first and third objections are not significant since in those groups in which there is no doubt whatever regarding the identity of the parietal organ there is much difference in the relative time at which the parietal organ and epiphysis appear, although the parietal organ in the lizards always seems to be in advance of the epiphysis. The failure of the parietal organ to pass far dorsally may be explained by its distance in front of the epiphysis which does not lie ventral to it and which otherwise by its growth might push the parietal organ dorsally as it does for example in Lacerta. Besides this, the extreme development of the paraphysis caudad in such forms as Lacerta may also tend to displace the parietal organ toward the dorsal surface of the head. This last factor is wanting in Thamnophis because of the shorter paraphysis which does not insinuate itself beneath the parietal organ. The wide separation of the epiphysis and parietal organ constitutes a valid objection to the notion here put forth, for a similar relation has not been noted in any other type. There are two facts, however, which seem to make this objection less significant. The parietal organ is known in various forms to originate in slightly different places, as will be shown later; and it has also been noted in this study that the segment of the roof of the diencephalon lying between the epiphysis and parietal organ in the earlier stages of the garter snake exhibits a different histological structure from the rest and resembles more nearly that of the epiphysis itself. It

seems reasonable, on the whole, to regard the present organ as a parietal organ rather than one sui generis.

Another matter upon which evidence has been produced by the present study is the independence of the parietal organ and epiphysis.

The earlier view regarding the relationship between the two was that the parietal organ was pinched off from the distal end of the epiphysis (Strahl '84). Thus it would appear that the two organs were in the closest possible relation. A few years later Baldwin Spencer ('86), as a result of an extensive study of the parietal organ of many lizards, confirmed Strahl's conclusion, for in all the species studied the parietal organ and epiphysis seemed to be connected by means of the 'parietal stalk.' Beraneck ('87) studying the development of the parietal organ and epiphysis in Lacerta agilis was the first investigator to regard the two as independent, arising from two separate anlagen, one of which lay close in front of the other. Francotte ('96) recognized that the parietal organ might arise in two different ways. According to the first type of origin the anlagen of the parietal organ and epiphysis appear as independent buds from the roof of the diencephalon. The anterior one, the parietal organ, appears first and is larger than the posterior one, which develops into the epiphysis. In the beginning the parietal organ is larger than the epiphysis. According to the second type of origin, the posterior bud does not arise from the roof of the diencephalon but from the postero-dorsal border of the anterior one. Francotte regarded this latter type to be derived from the former which he thought was the more primitive. This apparent origin from the same outgrowth Francotte explained by assuming that the parietal organ elongates more rapidly than the epiphysis at first and drags the latter along with it so that the lip between the two at an early stage really represents the segment of the roof of the diencephalon which lay between them in the first place. This is also confirmed in a measure by Klinckowström ('93) on Iguana. In this lizard the roof of the diencephalon at one time exhibits a single evagination directed anteriorly, which is secondarily separated into two parts by a

ringlike furrow. The parietal organ is in this way cut off from the epiphysis. The subsequent growth of the epiphysis is not, however, in the direction at right angles to the furrow just mentioned, but dorsally so that the scar marking the earlier connection of the parietal organ and epiphysis comes to lie on the anterior wall of the epiphysis. This means, as can readily be seen, that the material from which the greater part of the definitive epiphysis is derived, lay originally posterior to that of the parietal organ just as is the case where there are two separate anlagen for these organs. The fundamental difference between the condition in Iguana and Francotte's first type of origin of these organs lies in the greatly retarded appearance of the epiphysis in Iguana, until after the parietal organ's anlage has grown to considerable size.

Further evidence of the independence of these two structures is afforded by a study of the innervation of the epiphysis and parietal organ in certain vertebrates. The parietal organ may be supplied by the parietal nerve whose fibers enter the brain by way of the superior commissure, in front of the epiphysis, and from there may be traced to the right ganglion habenulae (Strahl and Martin '88); the epiphysis may be supplied by a nerve, the pineal nerve, which enters the posterior surface of the epiphysis and arises from the roof of the brain from the posterior commissure (Klinckowström '93, on Iguana).

The development of the parietal organ and epiphysis in the garter snake leaves no room for doubt as to the complete independence of these organs in this form; since there is a considerable interval between them on the roof of the diencephalon from their earliest appearance, in which space the superior commissure later appears.

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THE GASTRIC VASA BREVIA

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THIRTY-SEVEN FIGURES

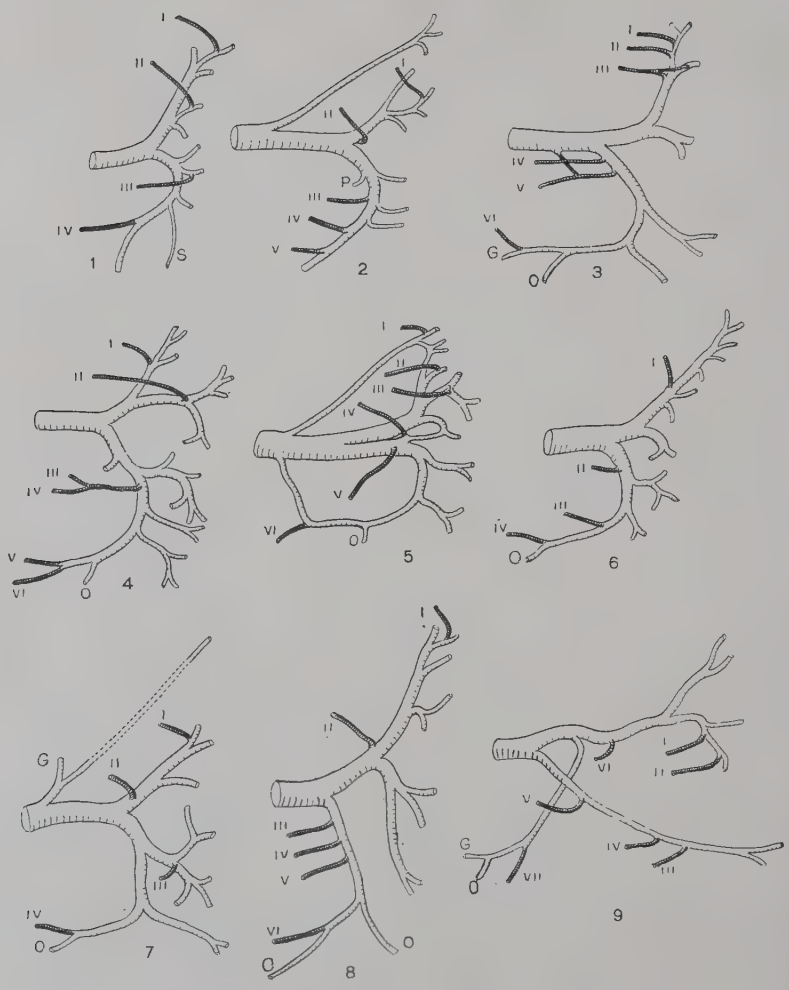
The gastric vasa brevia are those branches of the splenic artery and veins and their terminal divisions which pass by way of the gastro-splenic omentum to the fundus of the stomach.

In this consideration of the gastric vasa brevia the aim has been: first, to determine the most usual arrangement of these vessels in the adult, as regards number, size, origin, and distribution; and, second, to ascertain the time and manner of their development in the embryo. Conclusions regarding the adult arrangement are based on a series of twenty-five drawings of the spleens and splenic vessels of as many dissecting-room subjects. The first eight drawings were made by Dr. Bunting, and it was at his suggestion that the study was carried farther.

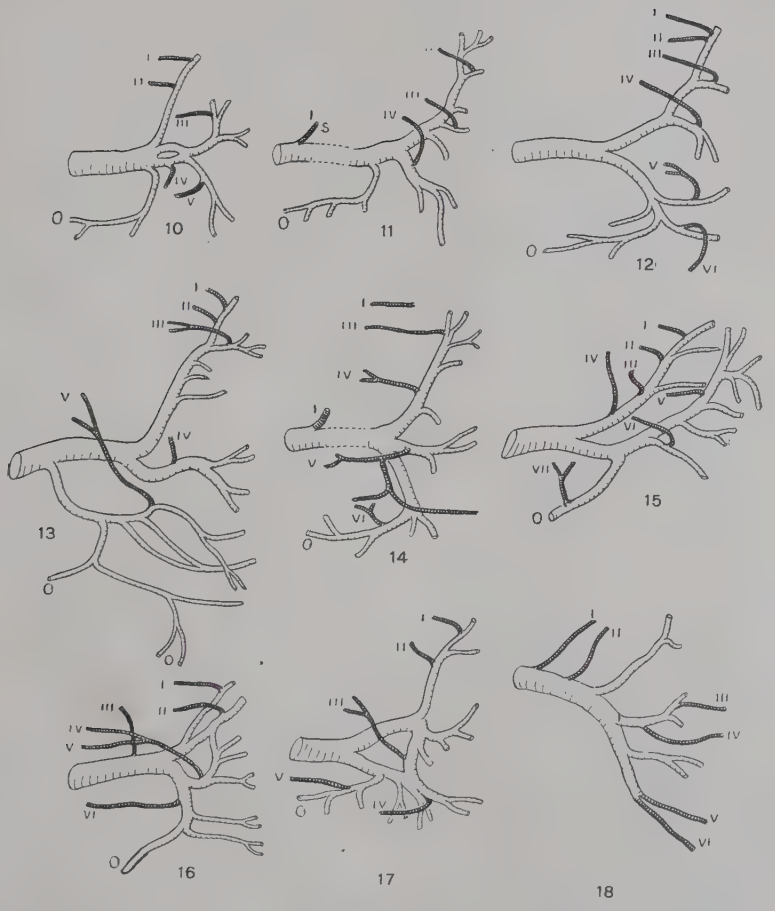
Number. A glance at the outstretched arteries (figs. 1–25), shows that there were three in two cases, four in six, five in six, six in eight, and seven in three. Thus there are usually more than three and seldom as many as seven; the most usual number is six, but four and five are hardly less frequent. The average number in the series was a little over five.

Size. The vasa brevia are always small. They were measured in fifteen of the subjects examined and in no case were they more than 4 mm. in diameter. Not infrequently they were mere threads, less than 0.5 mm. in diameter; the most common size was about 2 mm.

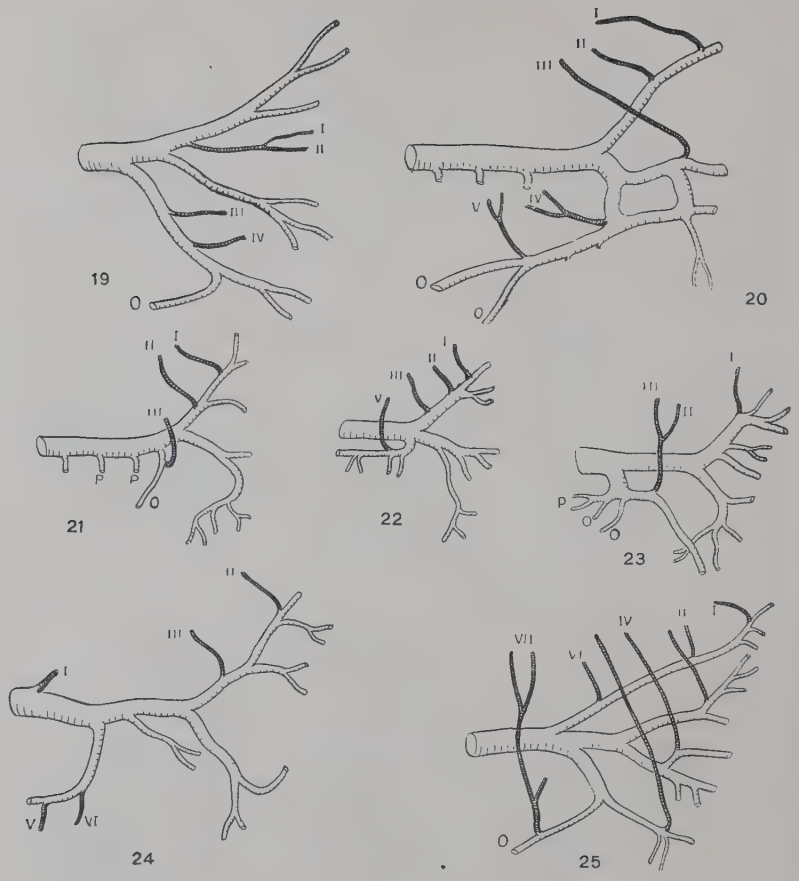
Origin. The splenic artery ordinarily divides into two main divisions, a superior for the supply of the upper half of the spleen, and an inferior for the supply of the lower half of the spleen, a part of the great omentum and a part of the greater curvature



Figs. 1–25 Diagrammatic sketches of twenty-five specimens showing the origin of the vasa brevia arteries of the stomach from the splenic artery and its branches. The vasa brevia are shown dark. The lighter branches not otherwise labeled are splenic branches. *O*, gastro-epiploic; *P*, pancreatic branch *S* (fig. 1), branch to accessory spleen.



of the stomach. The left gastro-epiploic may be a branch of the inferior division, as was true in thirteen cases, or it may be a branch of the main splenic trunk, occurring before the division into superior and inferior divisions. In any case the gastro-epiploic trunk usually gives off vasa brevia (e.g., this was true in thirteen of the seventeen gastro-epiploic vessels examined). It was true in every one of the eight instances in which the gastro-epiploic arose from the splenic artery proper.



There may be anastomosis between the superior and inferior divisions, as in figures 16 and 17, and there may be accessory superior branches from the splenic trunk, as in figures 2 and 5, or accessory inferior branches as in figure 9.

As we have seen, the vasa may arise from (1) the splenic artery itself; (2) the accessory splenic branches springing from the main splenic trunks midway between the coeliac axis and the spleen, and (3) the superior and inferior divisions (the latter including the gastro-epiploic) and their secondary branches.

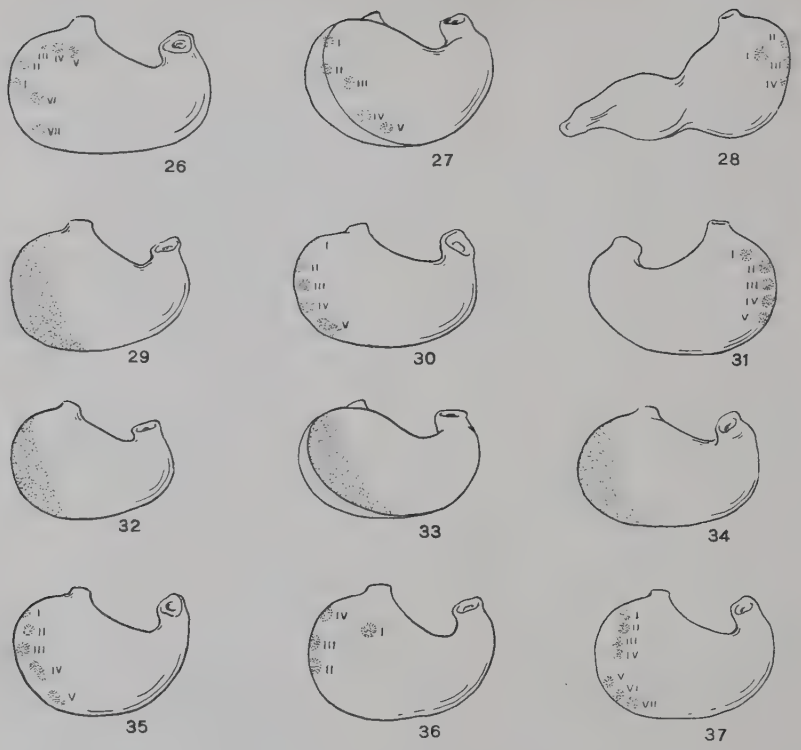
Vasa brevia arising from the splenic artery itself are the exception; figures 9 and 16 show them. That shown in figure 9 was about 1 mm. in diameter and it passed to the dorsum of the stomach, low down on the fundus (VI, fig. 26). That shown in figure 16 was larger (3 or 4 mm.) as were all the vasa brevia in this specimen. It passed to the dorsum of the stomach toward the cardiac orifice. Both these vessels arose close to the spleen. More frequently the splenic artery gives off a gastric branch near its origin. This branch may be a typical vas breve, but as often it is a coronary or accessory coronary branch destined for the supply of the lesser curvature. Such a branch was present in four of the twenty-five specimens, as shown in figures 11, 14, 18 and 24. In figure 11 the vessel was 1.5 mm. in diameter and about 5 cm. long. It arose 3 cm. from the origin of the splenic artery and 9 cm. from the hilus of the spleen, and passed to the dorsum of the fundus about 3.5 cm. below and 2 cm. to the left of the cardiac orifice. It did not anastomose with any other vessel; it was a true vas breve.

The vessel shown in figure 18 was similar in size, origin, and distribution; it was also a true vas breve. This specimen also showed a vas breve originating nearer to the spleen and similar to those described as occurring in figures 9 and 16.

In case of those splenic arteries which give off accessory splenic branches before reaching the spleen, the accessory branches almost always give rise to vasa brevia. Such branches were present in five cases, and all but one (fig. 2) gave off vasa brevia. But since these branches occur in but twenty per cent of the cases, we come to the rather self-evident conclusion, that typically, the vasa brevia arise from the superior and inferior splenic divisions and their branches.

We have said the usual number of vasa brevia is five or six. Table 1 shows the number of branches arising from the superior and inferior divisions.

The vasa brevia arising from the superior division tend to be smaller than those arising from the inferior. This was true in ten of the fifteen cases in which comparative measurements were made. In another case the smallest vessel arose from the supe-



Figs. 26–37 Diagrammatic sketches of twelve stomachs, showing the distribution of the vasa brevia of twelve of the specimens illustrated in figures 9 to 25. The distribution of the vasa brevia of the specimen shown in figure 9 is illustrated in figure 26; that of figure 10 in figure 27; figure 11 in figure 28; figure 12, in figure 29; figure 13, in figure 30; figure 14, in figure 31; figure 15, in figure 32; figure 17, in figure 33; figure 18, in figure 34; figure 20, in figure 35; figure 24, in figure 36; figure 25 in figure 37. In figure 36 the area of distribution of branch V was not determined accurately and is not shown. This is also true of branch VI in figure 31. In figures 29, 32, 33 and 34 the general area of distribution is shown instead of the approximate area of each branch. In figures 27 and 33 the stomach is turned so as to show the line of omental attachment. Figures 28 and 31 show the ventral, the other figures the dorsal surface of the stomach. In figures 28 and 31 the area of distribution of branch I is really on the dorsal surface so that the stomach is represented as transparent over this area. The other branches are distributed near the line of omental attachment.

TABLE 1

Figs.	1	2	3	4	5	6	7	8	9	10	11	12	13
Sup.	2	2	3	2	3	1	2	2	3	3	2	4	3
Inf.	2	3	3	4	2	3	2	4	4	2	1	2	2

Figs.	14	15	16	17	18	19	20	21	22	23	24	25
Sup.	3	4	2	2	2	2	3	2	3	1	2	4
Inf.	2	3	2	3	2	2	2	1	1	2	2	3

rior division, but the other superior branches were as large as the inferior. In the other four instances all the vessels were of about the same size. In many cases the superior branches, notably the first two, are mere threads, less than 0.5 mm. in diameter, whereas the inferior branches are apt to be 1.5 to 3 mm. in diameter.

A glance at the sketches shows that the point of origin of most of the vasa brevia is very uncertain so soon as one attempts to localize it to a secondary branch of the superior or inferior division. This is because the secondary splenic branches themselves are so variable. However, the first vas breve is relatively constant. It is small, as we have said, and usually arises from the highest splenic branch of the superior division—the terminal branch, virtually—close to where it sinks into the spleen. This was the case in sixteen of the twenty-five spleens examined; in another it arose slightly lower, from the superior division itself; in another it arose from the second instead of the first splenic branch; and in two others it arose from a superior accessory splenic branch. Its distribution is likewise relatively constant. Typically, it passes to the highest point on the fundus. It is not always the highest branch, however; thus in figure 15, vessel IV had the highest position on the stomach.

The second vas breve usually arises from the superior division or from one of its uppermost branches close to the first, runs parallel with the first, and has the next lower position on the fundus; like the first it is usually small. The third also usually

rises from the superior division in case there are five or six vessels in all. The fourth arises close to the bifurcation of the splenic artery, sometimes from one main division, sometimes from the other. The fifth and sixth arise from the inferior division, frequently from the gastro-epiploic trunk. The vessels tend to run parallel and to reach the stomach in the order of their origin.

Distribution. A consideration of the distribution of the vasa brevia gives a somewhat more satisfactory result. Since the vessels run in the gastro-splenic omentum, they reach the greater curvature of the stomach in the region of the fundus. Some small twigs may pass to the fundus just ventral to the line of omental attachment, but in every case virtually the whole area of vasa brevia supply was dorsal to the line of omental attachment: i.e., on the dorsal or original right side of the fundus. The uppermost vasa brevia tended to remain practically in the line of omental attachment; the lower branches, on the other hand, usually passed well onto the dorsum. In no case did a vessel pass much distance onto the ventral surface of the fundus.

In no case did a vas breve form anastomotic loops with other vessels. Thus they differ from all other gastric vessels, i.e., the coronary and gastro-epiploic branches; they are end arteries.

A glance at the sketches, figures 26 to 37, will indicate the location and extent of the area of distribution of the vasa brevia. In figure 31 the vessels are confined to the region of omental attachment, as many twigs passing anteriorly as posteriorly. No anterior twigs pass far, however, while the first vessel is distinctly dorsal in position. In figures 27 and 28, likewise, the vessels remain close to the line of omental attachment, though the tendency is toward dorsal distribution. In all other cases the area is distinctly dorsal to the line of attachment of the omentum. Furthermore, it is to the left of a line dropped from the esophagus to the greater curvature. That is to say, the vasa brevia are confined to the fundus. Figure 26 illustrates the fact previously mentioned that vessels arising from the inferior division do not necessarily take the lower positions on the stomach.

Development. The vasa brevia develop very early in the embryonic life as primary branches of the splenic artery. They

later become tributary to the splenic arteries as these are differentiated and in adult life are always small. Their number and origin is variable, but their distribution is constant: they pass practically wholly to the dorsum of the fundus. They are end arteries and in no case anastomose with other vessels. In a pair of duplicate twin fetuses there were in one body five vessels, in the other six and the origins of the vessels differed in the two specimens.

To summarize: In the adult there are usually five or six vasa brevia, but there may be fewer or more. The vessels usually arise from the superior and inferior divisions of the splenic artery, but they may arise from the main trunk of the splenic artery or from accessory splenic branches; the branches of the superior division tend to be smaller, more numerous and to take a higher position on the fundus than the inferior branches, but the reverse may be true. The vasa brevia are never very large—at least under normal conditions; they are terminal or end arteries; they pass to the dorsum of the fundus of the stomach.

MEMOIRS

OF

THE WISTAR INSTITUTE OF ANATOMY AND BIOLOGY

No. 5

THE DEVELOPMENT OF THE ALBINO RAT, MUS NORVEGICUS ALBINUS

G. CARL HUBER

From the Department of Anatomy, University of Michigan, and the Department of Embryology, the Wistar Institute of Anatomy and Biology

I. FROM THE PRONUCLEAR STAGE TO THE STAGE OF MESODERM ANLAGE; END OF THE FIRST TO THE END OF THE NINTH DAY

THIRTY-TWO FIGURES

CONTENTS

Introduction 3
Material and methods 5
Ovulation, maturation, and fertilization 9
Pronuclear stage 13
Segmentation stages 21
2-cell stage 21
4-cell stage 29
8-cell stage 31
12 to 16-cell stage 35
Summary of segmentation stages, rate, and volume changes 36
Completion of segmentation and blastodermic vesicle formation 42
Blastodermic vesicle, blastocyst, or germ vesicle 56
Late stages of blastodermic vesicle, beginning of entypy of germ layers 63
Development and differentiation of the egg-cylinder 73
Late stages in egg-cylinder differentiation, and the anlage of the mesoderm 92
Conclusions 108
Literature cited 112

II. ABNORMAL OVA; END OF THE FIRST TO THE END OF THE NINTH DAY

TEN FIGURES

CONTENTS

Introduction 115
Half embryos in Mammalia 117
Degeneration of ova at the end of segmentation 120
Incomplete or retarded segmentation 121
Abnormal segmentation cavity formation 126
Degeneration of ova as a result of pathologic mucosa 129
Imperfect development of ectodermal vesicle 132
Two egg-cylinders in one decidual crypt 138
Conclusions 140
Literature cited 142

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ON THE INFLUENCE OF EXERCISE ON THE GROWTH OF ORGANS IN THE ALBINO RAT

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For the past three years experiments have been carried on to determine the effect of long-continued exercise on the growth of organs in the albino rat. The main object of the present investigation was twofold: (1) to repeat the observations of Donaldson ('11) who found a slight increase (2.6 per cent) in the brain weight in albino rats which had been subjected to exercise for the period of six months, and (2) to extend the observations to other organs besides the central nervous system. The present paper includes the data obtained by the previous study, just mentioned, as well as the results of my own investigations.

TECHNIQUE

The opportunity for exercise was given by placing the test rats in a form of cage which was used by Slonaker ('08) in his studies on the daily activity of the albino rat. The revolving cage consists of a large cylindrical drum 58.5 inches in circumference, made of $\frac{3}{16}$-inch wire mesh, which revolves on a stationary axle. On the axle was fastened the nest box and the food and water pans. The number of revolutions of the cage is registered by a cyclometer.

Albino rats one month old were placed in these cages for a period of three to six months, which is equivalent to seven to fourteen years of human life. Each cage contained a single rat. The rats used for the control were litter brothers and sisters of those in the revolving cages and were placed in the ordinary laboratory cages (one foot high, one foot wide and six feet long). The total number of rats examined was 36 controls

and 42 test animals. For the material of the 1914 series the present writer is under great obligation to Miss Caroline Holt, a graduate student at The Wistar Institute, who permitted the use of her exercised rats with their controls, and I wish to thank her for her courtesy in this matter.

METHOD OF COMPUTING THE AMOUNT OF ALTERATION

In determining the deviations of the organs in the exercised rats from those in the controls, the following method was used: As a first step, the weights of the various organs corresponding to the observed body length of the rats were computed by means of formulas (for various formulas see Hatai '13 and '14). This computation was made for both the controls and the exercised rats. The differences between the observed and computed values of both control and exercised are now transformed into percentages by taking the computed values as 100 per cent. Thus we obtain two sets of percentage values, one expressing the difference between the computed and observed values in the control rats, and the other expressing the difference between computed and observed values in the exercised rats. If exercise has not altered the organs of the animals at all, then these two sets of percentages should be alike within the limits of the normal fluctuations. If, on the other hand, exercise has altered the organs, these two sets of percentages should differ more or less according to the nature of the response to exercise. If in the case of any organ we now take the difference between the percentage value obtained for the controls and that for the exercised rats, this difference represents the amount by which the exercised rats, as compared with controls, depart from the value obtained by the formula. By the use of this procedure, successive series are thus referred to the formula values in each instance and since the deviations are measured by this means always from the same standard, they may be directly compared with one another.

In the case of the thymus gland, the age of the rats was taken as the basis for the computation, since the weight of the thymus is much more highly correlated with the age than with either the

weight or the length of the body (Hatai '14). The example taken from the 1911 male series (the second series in table 3), may serve to illustrate the method of comparison described above (table 1). Expressing in words the results as given in the last line of this table, these show that the exercised rats are 13.4 per cent heavier than the controls and have a tail 1.62 per cent longer.

AMOUNT OF EXERCISE TAKEN

The rats in the revolving cages often take a large amount of voluntary exercise. To illustrate this I have chosen an example from the 1912 series and given the average distance run during every 24 hours for the entire period of 93 days.

As will be seen from table 2, the distance run is almost incredible in some instances, the greatest average run for 93 days being 10 miles per 24 hours; a record made by one female. Since the rat is most active during the night (Slonaker '12) this daily run

TABLE 1

	BODY LENGTH (MM.)	TAIL LENGTH (MM.)	BODY WEIGHT (GMS.)
Controls: observed values	212	176	238.3
Controls: values calculated from formulas (body length taken as basis of computation)		180	238.1
Percentage deviation of observed from calculated values.....A		−2.22%	0.08%
Exercised: observed values	195	164	202.0
Exercised: values calculated from formulas (body length taken as basis of computation)		165	178.1
Percentage deviation of observed from calculated values.....B		−0.60%	13.48%
Amounts by which the percentages for the exercised animals differ from those for the controls; i.e., B − A		1.62%	13.40%

TABLE 2

Showing the distance run by the exercised rats in a period of 93 days

EXERCISED RAT, NO.	NO. OF MILES PER 24 HOURS	SEX	EXERCISED RAT, NO.	NO. OF MILES PER 24 HOURS	SEX
8 B_{10}	0.4	M.	7 A_5	7.6	M.
7 A_{47}	0.5	M.	7 A_4	7.6	M.
8 B_9	0.6	M.	7 B^2_{17}	6.2	F.
7 B^2_{16}	0.6	M.	7 B_{20}	7.4	F.
7 B_{19}	4.8	M.	6 B^2_{92}	7.7	F.
7 B_{48}	6.5	M.	6 B^2_{83}	8.3	F.
6 B^2_{82}	6.7	M.	8 B_{11}	10.2	F.

was accomplished for the most part within a twelve-hour period. With the exception of the first four sluggish male rats, the average run was about $6\frac{1}{2}$ miles for males and 8 miles for females. Slonaker found that female rats were more active than the males and he further noticed considerable individual variation in the activities. The present results agree nicely with the observations of Slonaker. It is interesting to note also that the maximum average run by Slonaker's rats was 11 miles (average for one month) while that of mine was 10 miles per day for 93 days, thus showing a close agreement even in this respect. We do not know how active the wild Norway rats may be, but a considerable curtailment of the normal activity in the albino rats under domestication seems highly probable.

The effects of long-continued exercise on the body of the Albino as a whole, and on the organs, was the object of the present investigation.

INFLUENCE OF EXERCISE FOR 90 TO 180 DAYS ON THE EXTERNAL MEASUREMENTS AND ON THE ORGAN WEIGHTS

1. Alterations of the external measurements

The external measurements of the exercised albino rats contrasted with those of the controls are given in table 3.

To prevent misunderstanding or misinterpretation, a word of explanation touching the tables is in order. Using the series for 1911 males, the second one in table 3 (the same which has been used as an illustration for procedure on page 649), attention

is called to the following points: The entries for the control are the *observed* values—the entries for the exercised are the *observed* values. The percentages deviations of both controls and exer-

TABLE 3

Showing the external measurements in both control and exercised rats

	LENGTH (mm.) OF		WEIGHT OF BODY: GRAMS	DURATION OF EXERCISE: DAYS	AGE: DAYS	NO. OF RATS USED
	Body	Tail				
Stock albino rat (Donaldson, '11) M. and F.						
Control	199	165.00	199.60	180	242	31
Exercised	195	163.00	192.80		242	24
Per cent: Exerc.–cont.		0.42	2.90			
Stock albino rat, 1911 series M.						
Control	212	176.00	238.30	180	215	21
Exercised	195	164.00	202.00		195	11
Per cent: Exerc.–cont.		1.62	13.40			
Inbred albino rat, 1912 series M.						
Control	212	184.00	217.30	180	212	9
Exercised	214	181.00	245.30		213	10
Per cent: Exerc.–cont.		−2.77	8.42			
Inbred albino rat, 1912 series F.						
Control	191	174.00	155.40	180	215	6
Exercised	198	173.00	179.80		213	7
Per cent: Exerc.–cont.		−4.77	2.52			
Stock albino rat, 1914 series M.						
Control	176(F)	167.00	145.60	90	135	3
Exercised	198	178.00	220.90		135	4
Per cent: Exerc.–cont.		−2.56	11.35			
Stock albino rat, 1914 series F.						
Control	176	167.00	145.60	90	135	3
Exercised	182	171.00	159.40		135	4
Per cent: Exerc.–cont.		−1.60	−1.87			
Percentage by which exercised rats differ from controls. Same weight given to each series		−2.02	6.76			

cised from the formula values have been determined but *are not entered* in the table. The difference between these two percentage deviations is alone given in the table after '%: exerc.–contr.' To test the correctness of these last figures it is always necessary to carry out the operations which have been described (p. 648). This same explanation applies to the other series in this table and also to the other tables 3, 4 and 5.

Body length. The average absolute length of the body is practically identical in both the exercised and control rats. The difference amounts to 0.5 per cent in favor of the controls. The data given by Donaldson ('11) for a single series show also a small difference of 2 per cent in favor of the control. We may conclude therefore that exercise does not alter the growth of body in length to any noticeable extent.

Tail length. The tail length with respect to body length tends to be slightly shorter in the exercised than in the non-exercised rats. The average difference is 2.02 per cent in favor of the control. The data given by Donaldson show practical identity in his series. However, the difference is noted in four out of my five series and I conclude therefore that exercise tends to retard the growth of the tail in length.

Body weight. A slight increase of 6.76 per cent is given in the average body weight for the exercised rats when compared with that of the non-exercised. This difference appears in four series out of five. Data given by Donaldson shows also an increase of 2.90 per cent in favor of the exercised. This relative gain in body weight of the exercised rats may be due in part to the absence of lung disease in the exercised rats. As will be seen later, most of the control rats were suffering from a lung infection, while most of the exercised rats were free from this. It is therefore possible that the increased body weights shown in table 3 are in some measure due to the slightly emaciated condition of the control rats, thus raising the relative value in favor of the exercised rats. I am therefore inclined to believe that in the case of the albino rat the body weight is not much affected by the form of exercise here given—though it may be slightly increased.

Considering these three external characters together, we may say that long-continued exercise does not modify significantly any of the characters here mentioned with the possible exception of the tail length, which shows a slight tendency to a deficit with respect to the body weight.

2. Alterations of the viscera

TABLE 4

Showing the weights of viscera of the exercised rats compared with those of the controls. Arrangement of data explained on p. 650.

	BODY LENGTH (mm.)	HEART	WEIGHTS (GMS.) OF				ALIM. TRACT	NO. OF RATS USED
			Kidneys	Liver	Spleen	Lungs		
Stock albino rat, 1911 series, M.								
Control	212	0.886	1.768	10.21	0.611	1.796		21
Exercised	195	0.904	1.867	10.35	0.589	1.588		11
Per cent: Exerc.–cont.		26.980	32.170	23.15	25.980	17.250		
Inbred albino rat, 1912 series M.								
Control	212	0.784	1.627	8.50	0.445	2.325	7.86	9
Exercised	214	0.874	2.032	11.36	0.415	1.228	9.15	10
Per cent: Exerc.–cont.		7.380	17.300	22.46	−6.790	−82.990	9.49	
Inbred albino rat, 1912 series F.								
Control	191	0.587	1.246	6.48	0.395	2.205	6.77	6
Exercised	198	0.787	1.530	8.85	0.363	0.999	8.12	7
Per cent: Exerc.–cont.		17.430	8.310	17.24	−14.900	−89.970	7.52	
Stock albino rat, 1914 series M.								
Control	(F)176	0.595	1.054	6.19	0.651	1.000	8.27	3
Exercised	198	1.044	1.790	9.06	0.444	1.128	8.82	4
Per cent: Exerc.–cont.		37.680	25.280	13.12	−61.870	−15.160	−14.80	
Stock albino rat, 1914 series F.								
Control	176	0.595	1.054	6.19	0.651	1.000	8.27	3
Exercised	182	0.822	1.317	7.74	0.457	1.105	8.09	4
Per cent: Exerc.–cont.		27.130	11.930	12.72	−63.210	1.390	−9.76	
Average percentage by which exercised albino rats differ from controls. Same weight given to each series		23.320	19.000	17.74	−24.160	−33.090	−1.89	

From table 4 we note the following modifications.

Heart. In all the series the weight of the heart is considerably heavier in the exercised rats than in the controls. The average difference is 23.32 per cent in favor of the exercised rat.

Kidneys. The kidneys of the exercised rats are also heavier than those of the controls in all the series. We note the average difference of 19 per cent in favor of the exercised.

Liver. The weight of the liver is also heavier in the exercised rat in all the series. The difference is 17.74 per cent in favor of the exercised rat.

Spleen. On the other hand, the weight of the spleen is greater in the control than in the exercised. The difference amounts to as much as 24.16 per cent in favor of the controls. This difference does not appear to be due to a greater variability of the spleen, since it occurs in four series out of five, and furthermore, the same phenomena occurs in another series, which will be considered later (table 7). The reason why exercise retards the normal growth of the spleen with respect to body length is not clear.

Lungs. We notice the average difference of minus 33.90 per cent in the exercised lungs compared with the controls. In the case of the lungs, however, those heavier than normal for the body weight are associated with a lung infection. As a matter of fact, most of the control rats were infected, while the exercised rats were free from infection. It has already been noted that the infection of the lungs in the control rats was probably responsible in part for the relatively small body weight of the controls. It is highly interesting to see that exercise prevents, or at least delays, an onset of a very prevalent pulmonary infection in the albino rat.

Alimentary tract. The alimentary tract as here designated includes not only the digestive tract proper, such as the stomach, intestine, etc., but also all attached structures, as the pancreas, omentum, as well as fat deposited in them. As is shown in table 4, the alimentary tract is not evidently modified. We note an average difference of 1.89 per cent in favor of the controls. This small difference, associated as it is with the bal-

anced distribution of plus and minus variations, justifies our conclusion that exercise has not affected this part of the visceral system.

3. Alterations of ductless glands

Testes. The testes of the exercised rats show an average increase of 12.33 per cent when contrasted with those of the controls. This increase occurs in both the male series, thus showing the significance of the reaction.

Ovaries. The ovaries in the exercised rats show an increase of 84.33 per cent when contrasted with those of the controls. The difference between the exercised and controls in these organs is evident even at a glance. It is interesting to note that the sex glands of the Norway rats are normally heavier than those of the Albinos. The increase here shown as the result of exercise may possibly indicate a return to the wild form, not in size alone but also in fertility.

Hypophysis. The hypophysis responds to exercise differently according to sex. We note an increase of 10.25 per cent in the case of the male and a deficit of 22.23 per cent in the case of the female. The approach of the weights in the two sexes and the larger loss in the female bring about relations which I have observed in the wild Norway (Hatai '14 b).

Suprarenal glands. As in the case of the hypophysis, the suprarenal glands show also dissimilar reaction to exercise according to the sex. Thus we note practically no alteration in the male (0.84 per cent), while there is an increase of 47.76 per cent in the female—again relations such as the wild Norway shows (Hatai '14 b).

Thyroid. We note a difference of nearly 13.44 per cent in favor of the control rats.

Thymus gland. The thymus of the exercised rat shows a slight relative increase of 4.80 per cent when contrasted with that of the control. It occurs, however, in only two cases out of four, and furthermore the greater variability in the alteration suggests that the difference here noted may not be significant at all. We must await the results of future experiments to make any positive statement.

TABLE 5

Showing the weights of the ductless glands in the exercised rats compared with those in the controls. Arrangement of data explained on page 650.

	BODY LENGTH (mm.)	SEX GLANDS	WEIGHTS (GMS.) OF				NO. OF RATS USED
			Hypophysis	Suprarenals	Thyroid	Thymus	
Stock albino rats, 1911 series M.							
Control.....	212	2.2280					21
Exercised....	195	2.3380					11
Per cent: Exerc.–cont.		19.7800					
Inbred albino rat, 1912 series M.							
Control.....	212	2.3430	0.0085	0.0328	0.0344	0.0984	9
Exercised...	214	2.5030	0.0096	0.0339	0.0354	0.1085	10
Per cent: Exerc.–cont.		4.8800	10.2500	0.8400	0.2700	7.1800	
Inbred albino rat, 1912 series F.							
Control.....	191	0.0368	0.0113	0.0425	0.0273	0.1051	6
Exercised...	198	0.0602	0.0127	0.0622	0.0282	0.1698	7
Per cent: Exerc.–cont.		46.4200	−2.0200	27.3200	−5.4600	41.7000	
Stock albino rat, 1914 series M.							
Control.....	176 (F.)				0.0282	0.1931	3
Exercised...	198				0.0290	0.1355	4
Per cent: Exerc.–cont.					−25.8100	−25.4900	
Stock albino rat, 1914 series F.							
Control.....	176	0.0557	0.0076	0.0417	0.0282	0.1931	3
Exercised....	182	0.1145	0.0058	0.0656	0.0247	0.1836	4
Per cent: Exerc.–cont.		122.2500	−42.4300	47.7600	−22.7400	−4.2000	
Average percentage by which exercised albino rats differ from control. Same weight given to each series		12.33(M.)	10.25(M.)	0.84(M.)	−13.4400	4.8000	
		84.33(F.)	−22.23(F.)	47.76(F.)			

From the above it is clear that most of the ductless glands are subject to a considerable alteration as the result of exercise. Beyond pointing out that the exercised rats show, in the case of the testes, ovaries, hypophysis and suprarenals, relations similar to those found in the wild Norway, I am unable to give an interpretation of the changes observed. The data are therefore presented without further comment except to repeat that the alterations here noted are constant and are not the result of a great inherent variability of these organs.

4. Alterations of central nervous system and of eyeballs

Brain weight. On the average the brain weight of the exercised rat is 4.02 per cent heavier than that of the controls. This relatively greater weight of the exercised rat is true not only on the average, but also for all the series given in table 6. A variation of 4 per cent is not usually regarded as a large figure, nevertheless it is certainly significant for this particular organ. Indeed, this gain of 4 per cent is the largest plus alteration so far obtained from our experiments. It seems safe to conclude from its constancy, as well as from relative uniformity of the value, that exercise increases the brain weight with respect to the body length. It should be noted also that the present results agree with the finding of Donaldson ('11) in this respect. It is not clear, however, whether this gain was due to a uniform enlargement of an entire mass, or to the increase of special divisions or structural components of the encephalon. A detailed analysis may settle this question in the future.

Spinal cord weight. The weight of the spinal cord evidently is not significantly altered. This is shown not only by its slight average modification of 0.88 per cent but also by the fact that the variation is not uniform in all the series. Donaldson found a difference of 0.65 per cent in favor of the control rat. All we can say about this part of the central nervous system is that exercise produces no significant alterations.

Amount of water in the brain and spinal cord. As shown in table 6, the percentage of water in the brain and spinal cord is

TABLE 6

Showing the weights of brain and spinal cord and of eyeballs of the exercised rats compared with those of the controls. Arrangement of data explained on p. 650.

	BODY LENGTH (mm.)	WEIGHTS (GMS.) OF		PERCENTAGE OF WATER		WEIGHT OF EYEBALLS (GMS.)	NO. OF RATS USED
		Brain	Sp. cord	Brain	Sp. cord		
Stock albino rat (Donaldson '11) M. and F.							
Control	199	1.920	0.597	78.41	71.45		31
Exercised	195	1.951	0.580	78.12	71.37		24
Per cent: Exerc.–cont.		2.570	−0.650	−0.29	−0.08		
Stock albino rat, 1911 series M.							
Control	212	1.872	0.614	78.09	70.39		21
Exercised	195	1.866	0.564	78.08	71.05		11
Per cent: Exerc.–cont.		3.670	3.000	−0.01	0.66		
Inbred albino rat, 1912 series M.							
Control	212	1.784	0.610	78.57	71.40	0.294	9
Exercised	214	1.868	0.603	78.40	71.20	0.299	10
Per cent: Exerc.–cont.		3.940	−2.420	−0.17	−0.20	0	
Inbred albino rat, 1912 series F.							
Control	191	1.715	0.547	78.24	70.89	0.288	6
Exercised	198	1.826	0.558	78.57	71.65	0.279	7
Per cent: Exerc.–cont.		4.430	−3.220	0.33	0.76	−9.920	
Stock albino rat, 1914 series M.							
Control	176(F)	1.648				0.288	3
Exercised	198	1.836				0.288	4
Per cent: Exerc.–cont.		5.990				−16.950	
Stock albino rat, 1914 series F.							
Control	176	1.648				0.288	3
Exercised	182	1.701				0.276	4
Per cent: Exerc.–cont.		2.060				−10.910	
Percentage by which exercised albino rats differ from controls. Same weight given to each series.		4.020	−0.88	−0.02	0.41	−9.45	

not modified. This result agrees with the findings of Donaldson ('11).

Eyeballs. As a sample of the sense organs, the eyeballs were examined. As will be seen from table 6, the average weight of the eyeballs of the exercised rats is 9.45 per cent less than that of the non-exercised rat. The meaning of the smaller eyeballs in the exercised rats is not at all clear. I may mention, however, that from the data so far accumulated, the wild Norway rat has somewhat smaller eyeballs than the Albinos of the same body length.

THE EFFECT OF EXERCISE TAKEN FOR A PERIOD OF 30 DAYS

We have found that exercise taken for a period of 90 days produces changes in the organs to the same extent as exercise given for the period of 180 days (tables 3 to 6). It was thought interesting to determine the minimum period necessary to produce all the typical alterations. For this purpose the rats one month old were kept in the revolving cages for 30 days. The number of rats used was 6 controls and 6 experimented.

Without discussing the individual characters separately, we may make the following general statement.

(1) In no case are the alterations as large as those shown by the rats which had been kept in the revolving cages for the period of 90 or 180 days.

TABLE 7

Showing percentage values by which the several characters of the rats exercised for 30 days differ from those of the non-exercised. Males = 3 controls and 4 exercised. Females = 3 controls and 2 exercised. In this table only the final percentage values (i.e., for "% exerc.-contr.") are given.

	PER CENT		PER CENT			PER CENT
Tail length	0.4	Heart	8.0	Thyroid		2.0
Body weight	2.4	Kidneys	8.2	Thymus		−1.1
Brain	0.2	Liver	−9.5	Hypophysis	M.	25.7
Eyeballs	4.2	Spleen	−52.9		F.	10.6
Alimentary tract	−7.7	Testes	9.2	Suprarenals	M.	8.0
Lungs	4.7	Ovaries	51.4		F.	30.1

(2) The amount of time necessary to produce the typical alterations varies according to different organs.

(3) While the heart and kidneys show a typical change, the liver shows a contrary modification. This may be due to a rapid utilization of reserve materials following a rapid growth, as well as the greater activity of the animal at this younger period.

(4) The early response of the sex glands to exercise may be the result of two combined factors; a greater supply of nutrition following the rapid circulation, and a strong tendency for growth of sex glands at this period of 50 to 60 days of age.

(5) Changes shown by other organs, particularly by the hypophysis, suprarenals and spleen, are very large. It is to be noted, however, that the weights of the hypophysis in the two sexes, despite the fact that both show a gain, tend to come together as in the 90 and 180 day series, while in the case of the suprarenals, the increase in the female is much the greater, a result again agreeing with the earlier series.

We may conclude from this short experiment that the effect of exercise is clearly shown in the rats which have been kept in the revolving cages for one month only, though the amount of modification varies considerably according to different organs.

TABLE 8

Showing the relation between heart weight and amount of exercise taken

DESIGNATION OF RAT	BODY LENGTH (mm.)	HEART WEIGHT (GMS.)	NO. OF MILES PER 24 HOURS	SEX
8 B_{10}	222	0.725	0.4	M.
7 A_{47}	212	0.771	0.5	M.
8 B_{9}	215	0.799	0.6	M.
7 B^{2}_{16}	218	0.853	0.6	M.
7 B_{19}	201	0.720	4.8	M.
7 B_{48}	220	0.888	6.5	M.
6 B^{2}_{82}	217	1.149	6.7	M.
7 A_{5}	205	0.907	7.6	M.
7 A_{4}	212	0.915	7.6	M.
7 B^{2}_{17}	198	0.745	6.2	F.
7 B_{20}	191	0.724	7.4	F.
6 B^{2}_{92}	205	0.838	7.7	F.
6 B^{2}_{83}	201	0.891	8.3	F.
8 B_{11}	197	0.762	10.2	F.

WEIGHT OF HEART IN RELATION TO THE AMOUNT OF EXERCISE TAKEN

The variability in the activities of rats in the revolving cage suggested that there might exist a definite relation between the heart weight and the amount of exercise taken. To test this point table 8 was prepared. The data were taken from the 1912 series.

Among normal rats kept in the ordinary cages the correlation between heart weight and body length is very high (Hatai '13). Table 8 shows, however, that the correlation between the heart weight and body length in the exercised rats is almost zero, while, on the other hand, the correlation between the heart weight and amount of exercise taken is very high. To illustrate these points, I have divided the male records into three groups and the females into two groups according to the following plan:

Male	Group 1	Average for the first four sluggish rats
	Group 2	Average for the rats which ran 4.8 to 6.7 miles
	Group 3	Average for the rats which ran 7.6 miles
Females	Group 1	Average for the rats which ran 6.2 to 7.7 miles
	Group 2	Average for the rats which ran 8.3 to 10.2 miles

These average values are tabulated below.

		Body length (mm.)	Heart weight (gms.)	Mean distance run (miles)
Males	Group 1	217	0.787	0.5
	Group 2	213	0.919	6.0
	Group 3	209	0.911	7.6
Females	Group 1	198	0.769	7.1
	Group 2	199	0.827	9.3

From the above we notice that despite a greater body length in Group 1 (males) the corresponding heart weight is less in accordance with the least distance run. On the other hand, Group 3 (males) which has the least body length (209 mm.) gives almost as large a heart weight as Group 2, whose body length is 213 mm. In coincidence with this non-correlation

between the body length and heart weight, we notice a harmonious relation between the heart weight and amount of exercise taken.

In the female series we notice that despite the practical identity in their body length, Group 2, which had run the greater distance, surpasses in heart weight Group 1, which had run the lesser distance. These facts indicate clearly that the heart increased in weight in relation to the amount of exercise taken, as was anticipated.

GENERAL REMARKS

It is clear from the foregoing that long-continued exercise (equivalent to a period of 7 to 14 years in man) in the albino rat produces many striking alterations in the organs. The modifications here given are found to be true not only for all the series, but in most cases even for the contrasted pairs of rats, and thus the results are not dependent on the variability of these organs. I am confident that the alterations are the result of the long-continued exercise. It may not be out of place to mention here that a careful analysis of data has been made to see whether or not the infected lungs are in any way responsible for the changes observed in the organs. The results were negative.

The medical literature abounds with writings on the subject of 'exercise.' We find a universal recognition of hypertrophy of the heart following severe and long-continued exercise. I am not aware, however, that there are any similar statements concerning the modifications of other organs. Although from the results of physiological investigations on metabolism during or after severe physical exercise in man and in mammals, the occurrence of modifications in organs (such as the kidneys, liver, lungs, etc., besides the heart) are quite conceivable, yet we still lack the anatomical data for man.

From a purely biological standpoint, long-continued exercise has a special interest in the case of the domesticated albino rat. Former investigation has established the fact that the albino rat is a strain of the Norway rat (Hatai '07) and further, that these

two forms of the rat possess central nervous systems of a dissimilar weight, the Norway having an absolutely heavier brain and spinal cord for a given boby weight (Donaldson and Hatai '11). Again, recently, I have shown that the relative weights of some of the ductless glands differ also in the Norway and albino rats (Hatai '14 b).

In rabbits, Darwin ('83) noted several physical differences, particularly in the cranial capacity between the wild and domesticated forms. The wild rabbits possessed a noticeably greater cranial capacity than the domesticated variety. More recently Lapicque and Girard ('07) have accumulated extensive data on the brain weights in wild and domesticated races. These two authors conclude also that the wild forms surpass the domesticated in their relative brain weights. Domestication, however, involves numerous interrelated factors which can be only slowly isolated by systematic study, and this experiment was devised to test the value of exercise, which seems to be one of the important factors forming the complex of domestication. The present investigation shows that at least in such organs as the brain, eyeballs, sex glands, hypophysis and suprarenals, the exercised Albinos show an approach to the Norway rat.

In conclusion, I may repeat that from the anatomical side the question of exercise is usually taken rather lightly in the case of man, nevertheless when we consider its striking effect on some of the organs of the rat, a further careful investigation of the subject, not only in the rat but in man also, seems certainly worth while, both from the general biological standpoint and for its bearing on hygiene.

CONCLUSIONS

1. The following determinations were made on exercised as compared with non-exercised rats: (1) External measurements; body and tail length and body weight. (2) Visceral organs; heart, kidneys, liver, lungs, spleen and alimentary tract. (3) Ductless glands; testes, ovaries, hypophysis, suprarenals, thyroid

and thymus., (4) Nervous system and sense organs; brain and spinal cord, and eyeballs.

2. The albino rats allowed to exercise in the revolving cages for 90 or 180 days show modifications in most of the organs. Among them, the following may be mentioned:

(a) The heart, kidneys and liver show an average excess of about 20 per cent, while the spleen shows a similar amount of deficiency.

(b) The brain weight shows an average excess of 4 per cent, while no change is noticed in the case of the spinal cord. (This result agrees with the observation of Donaldson '11).

(c) The ovaries give an excess of 84 per cent, while the testes give an excess of 12 per cent.

(d) The hypophysis, as well as the suprarenals, respond differently to exercise according to sex. Furthermore, these two organs show, as the result of exercise, an approach to the relations characteristic for the Norway rat.

(e) The exercised rats were either entirely free from lung infection or but slightly affected. The control rats, on the other hand, had badly infected lungs and in some series several of them were lost, presumably from the lung disease. Analysis of the data shows that the lung infection is not responsible for the changes observed in the organs.

3. Exercise for the period of 30 days showed in most organs modifications similar to those observed in rats exercised for 90 to 180 days.

4. In the exercised rats the heart weight and amount of exercise taken are highly correlated.

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MEMOIRS

OF

THE WISTAR INSTITUTE OF ANATOMY AND BIOLOGY

No. 6

THE RAT

COMPILED AND EDITED BY

HENRY H. DONALDSON

REFERENCE TABLES AND DATA FOR THE ALBINO RAT (MUS NORVEGICUS ALBINUS) AND THE NORWAY RAT (MUS NORVEGICUS)

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PREFACE

For a number of studies on the growth of the mammalian nervous system made by my colleagues and myself we have used the albino rat. In the course of the work we frequently felt the need of referring to other physical characters of the rat to which the nervous system might be related. This led us to collect such data as were already in the literature and also led us to make further investigations. The facts gathered in this way have proved useful to us and are here presented in the hopes that they will be useful to others also.

CONTENTS

Preface. Introduction. Classification. Early records and migrations of the common rats.

Part 1. Albino rat—Mus norvegicus albinus. Chapter 1—Biology. Chapter 2—Heredity. Chapter 3—Anatomy. Chapter 4—Physiology. Chapter 5—Growth in total body weight according to age. Chapter 6—Growth of parts or systems of the body in weight. Chapter 7—Growth of parts and organs in relation to body length and weight in relation to age. Chapter 8—Growth in terms of water and solids. Chapter 9—Growth of chemical constituents. Chapter 10—Pathology.

Part 2. Mus norvegicus. Chapter 11—Life history. Chapter 12—Growth in weight of parts and systems of the body. Chapter 13—Length of tail and weights of body, brain and spinal cord in relation to body length. Chapter 14—Growth in terms of water and solids. Chapter 15—References to the literature. Index

THE GROWTH OF THE FETUS OF THE ALBINO RAT FROM THE THIRTEENTH TO THE TWENTY-SECOND DAY OF GESTATION

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TWO FIGURES

For the prenatal growth in weight of the human body Jackson ('09) has presented data gathered by himself and compared these with such data as had already been published. Similarly, Lowrey ('11) has studied the prenatal growth of the pig. In both cases the authors have found it necessary to depend in part on preserved material. While preservation may not alter materially the relative weights of parts of the body, it undoubtedly does alter the total body weight and the records for that character must be interpreted, therefore, with this fact in mind.

The following study on the growth of the fetus of the albino rat forms another series of observations on the prenatal growth of the mammal and has the special virtue of being made throughout on fresh specimens.

The fetuses were all from second litters, the female having been allowed to breed once and to raise her litter under observation, so that we might be assured of her normal behavior as a breeding animal. The data have been gathered from the colony at The Wistar Institute between 1907 and 1913.

METHODS

The female was mated for the second time, under observation, and after the lapse of the desired interval, was killed with ether. The fetuses were removed, cleared of membranes, and then each placed in a previously weighed stoppered vial and the weight determined to a tenth of a milligram. The operation was al-

ways conducted within a protecting chamber to prevent the loss of moisture by evaporation. The fetus of 13 days was found to be the youngest which would stand manipulation without damage and the observations begin with that age. The litters of 38 females have been thus studied. The total number of fetuses removed was 336, giving an average of 8.8 per litter, with a range of from 3 to 16 fetuses per litter. For 330 of these the exact weights have been obtained.

The observations furnish records for the weights of the fetus from the 13th to the 22d day inclusive—the latter being about the time of birth—under usual conditions, and within these limits they give the weights of the fetus at approximately twenty-four-hour intervals. The observed weights for this series are entered in table 1.

When the data of table 1 are combined and the means taken, we obtain the mean fetal weights given in table 2. The values given in table 2 are the means of the averages for the several litters of like age. Thus the average value for each litter was given the same weight irrespective of the number of fetuses in the litter. When the data of table 2 are plotted they furnish the graph in chart 1. The form of this graph illustrates the rate of growth as given in table 2 and this agrees with the general observation that in the growing fetus the rate tends to diminish with advancing age.

It has been pointed out by Donaldson ('06) that we may assume the span of life in the albino rat to be three years—between birth and natural death—and that this span in the rat is equivalent to ninety years in man. On this assumption the rat grows thirty times as rapidly as man. If we apply this ratio to the gestation period it follows that one-thirtieth of the human gestation period is about 9 days, but the rat has a gestation period of some 22 days. The explanation of this discrepancy between the rate of prenatal and that of postnatal growth is still wanting but the recent observations of Huber ('15) on the early stages of development in the Albino show that the first phases go very slowly. Taking 22 days for the gestation period of the Albino and 271 days (Mall, in Keibel and Mall '10) for

TABLE 1

Giving the observed weights of the fetuses at different ages from the 13th to the 22d day of gestation. Where the horn of the uterus from which the fetus came and its relative position in the horn were not noted, the fetus weights are given in ascending values under the heading 'Horn and position not noted.' When these facts were noted the weights of the fetuses are given under the respective horns and in serial order, no. 1 being the fetus nearest to the ovary. In a few cases the horn was noted but the order of the fetuses not determined. All the weighings were made to the tenth of a milligram, but in the table only three digits are entered. The diet of the mother, which appears to influence the number of fetuses, is also given

SERIAL NO.	AGE OF LITTER		DIET	HORN OF UTERUS AND POSITION IN HORN		HORN AND POSITION NOT NOTED
	Days	Hours		Left	Right	
39....	13		Scrap	0.036 1	1	
				0.038 2	0.045 2	
				0.044 3	0.038 3	
					0.029 4	
					0.031 5	
21....	13	2	Bread and milk	0.— 1	0.010 1	
				0.— 2	0.055 2	
				0.041 3	0.028 3	
					0.068 4	
					0.037 5	
					0.042 6	
					0.047 7	
22....	13	2	Bread and milk	0.032	0.033	
				0.034	0.043	
				0.034	0.050	
				0.036		
				0.038		
				0.041		
				0.—		
23....	13	2	Bread and milk	0.046 1	0.058 1	
				0.046 2	0.049 2	
				0.036 3	0.046 3	
				0.049 4	0.038 4	
				0.041 5		
				0.046 6		

TABLE 1 (Continued)

SERIAL NO.	AGE OF LITTER		DIET	HORN OF UTERUS AND POSITION IN HORN		HORN AND POSITION NOT NOTED
	Days	Hours		Left	Right	
42....	14		Scrap	0.092 1	0.081 1	
				0.088 2	0.108 2	
				0.093 3	0.107 3	
				0.107 4	0.085 4	
				0.092 5	0.101 5	
					0.091 6	
					0.097 7	
					0.104 8	
					0.059 9	
17....	14	2	Bread and milk	0.122 1		
				0.145 2		
				0.098 3		
				0.127 4		
				0.116 5		
				0.136 6		
				0.101 7		
20....	14	2	Bread and milk	0.117 1	0.085 1	
				0.— 2	0.099 2	
				0.135 3	0.131 3	
24....	14	2	Bread and milk	0.103 1	0.108	
				0.144 2	0.101	
				0.115 3	0.091	
				0.120 4	0.096	
				0.100 5	0.102	
					0.104	
14....	14	2	Bread and milk			0.080
						0.109
						0.118
						0.119
						0.121
						0.124
						0.126
43....	15		Scrap	0.104 1	0.119 1	
				0.109 2	0.098 2	
				0.114 3	0.111 3	
				0.094 4	0.088 4	
				0.132 5	0.109 5	
				0.118 6	0.097 6	

TABLE 1 (Continued)

SERIAL NO.	AGE OF LITTER		DIET	HORN OF UTERUS AND POSITION IN HORN		HORN AND POSITION NOT NOTED
	Days	Hours		Left	Right	
38....	15		Scrap	0.223 1	0.228 1	
				0.202 2	0.217 2	
				0.205 3	0.244 3	
				0.217 4		
				0.206 5		
16....	15		Bread and milk	0.148	0.158	
				0.167	0.170	
				0.182	0.176	
				0.183	0.189	
				0.197	0.190	
				0.226		
7....	15		Bread and milk			0.119
						0.143
						0.176
						0.186
						0.193
						0.196
41....	16		Scrap	0.319 1	0.342 1	
				0.306 2	0.360 2	
				0.336 3	0.336 3	
				0.329 4	0.327 4	
				0.315 5	0.322 5	
				0.256 6		
15....	16		Bread and milk	0.348 1	0.258 1	
				0.310 2	0.306 2	
				0.322 3	0.306 3	
				0.347 4	0.353 4	
				0.300 5	0.288 5	
12....	16		Bread and milk			0.257
						0.291
						0.336
25....	16		Bread and milk			0.320
						0.326
						0.328
						0.332
						0.351
						0.352
						0.356
						0.373
						0.390

TABLE 1 (Continued)

SERIAL NO.	AGE OF LITTER		DIET	HORN OF UTERUS AND POSITION IN HORN		HORN AND POSITION NOT NOTED
	Days	Hours		Left	Right	
5.....	16		Bread and milk			0.220 0.233 0.237 0.252 0.263 0.269 0.274 0.276 0.298 0.304 0.311
18....	17		Bread and milk	0.536 1 0.474 2 0.617 3 0.543 4	0.419 1 0.529 2 0.608 3	
40....	17		Scrap			0.482 0.491 0.493 0.508 0.530 0.531 0.543 0.625
6.....	17		Bread and milk			0.518 0.536 0.580 0.595 0.649 0.650
13....	18		Bread and milk			0.898 0.934 0.955 0.101 0.105 0.105 0.106 0.108

TABLE 1 (Continued)

SERIAL NO.	AGE OF LITTER		DIET	HORN OF UTERUS AND POSITION IN HORN		HORN AND POSITION NOT NOTED
	Days	Hours		Left	Right	
30....	18		Scrap			0.825
						0.938
						0.941
						0.944
						0.958
						0.961
						0.962
						0.973
						0.978
						0.980
						0.983
						0.986
						1.000
						1.010
						1.020
						1.090
4.....	18		Bread and milk			0.930
						0.950
						1.030
						1.020
						1.090
						1.130
						1.170
						1.230
						1.250
36....	18		Scrap			0.819
						0.859
						0.866
						0.939
						0.943
						0.954
						0.961
						0.967
						1.010
						1.150
37....	19		Scrap	1.480 1	1.310 1	
				1.550 2	1.690 2	
				0.530 3	1.540 3	
				1.450 4	1.340 4	

TABLE 1 (Continued)

SERIAL NO.	AGE OF LITTER		DIET	HORN OF UTERUS AND POSITION IN HORN		HORN AND POSITION NOT NOTED.
	Days	Hours		Left	Right	
19....	19		Bread and milk	1.930 1	1.560 1	
					2.020 2	
					1.740 3	
					1.910 4	
					1.630 5	
					1.860 6	
					1.900 7	
2.....	19		Bread and milk	1.020		
				1.440		
				1.440		
				1.550		
31....	19		Scrap			1.510
						1.590
						1.670
						1.670
						1.690
						1.700
						1.710
						1.730
						1.730
						1.740
35....	20		Scrap	2.280 1	2.780 1	
				2.310 2	2.480 2	
				2.700 3	2.520 3	
				2.520 4	2.690 4	
				2.390 5		
				2.510 6		
33....	20		Scrap			2.130
						2.280
						2.470
						2.480
						2.500
						2.550
						2.600
26....	20		Scrap			2.770
						2.830
						2.870
						2.900

TABLE 1 (Continued)

SERIAL NO.	AGE OF LITTER		DIET	HORN OF UTERUS AND POSITION IN HORN		HORN AND POSITION NOT NOTED
	Days	Hours		Left	Right	
26....	20		Scrap			2.940
						3.000
						3.060
						3.200
34....	21		Scrap	3.750	3.980	
				3.950	4.050	
				4.000	4.280	
				4.020		
				4.160		
				4.420		
35....	21		Scrap			3.920
						3.990
						4.030
						4.110
						4.150
						4.220
32....	21		Scrap			3.580
						3.720
						3.790
						3.810
						3.930
						4.080
						4.090
						4.260
						4.370
28....	21		Scrap			3.030
						3.400
						3.470
						3.470
						3.550
						3.580
						3.590
						3.720
						3.760
						3.950
27....	21		Scrap			4.000

TABLE 1 (Continued)

SERIAL NO.	AGE OF LITTER		DIET	HORN OF UTERUS AND POSITION IN HORN		HORN AND POSITION NOT NOTED
	Days	Hours		Left	Right	
27....	21		Scrap			4.020 4.120 4.150 4.220 4.330 4.380 4.460
44....	22		Scrap	4.460 1 4.710 2	3.910 1 4.710 2 4.950 3 4.700 4 4.540 5 4.820 6 4.750 7 4.710 8	

TABLE 2

Derived from the data in table 1, and showing the mean weights of the fetuses at ten ages during gestation

AGE IN DAYS	NUMBER OF FETUSES	AVERAGE WEIGHT OF FETUS IN GRAMS	RATE OF INCREASE IN WEIGHT
			per cent
13	34	0.040	
14	44	0.112	179
15	37	0.168	50
16	44	0.310	83
17	21	0.548	77
18	43	1.000	83
19	30	1.580	58
20	25	2.630	65
21	42	3.980	51
22	10	4.630	16

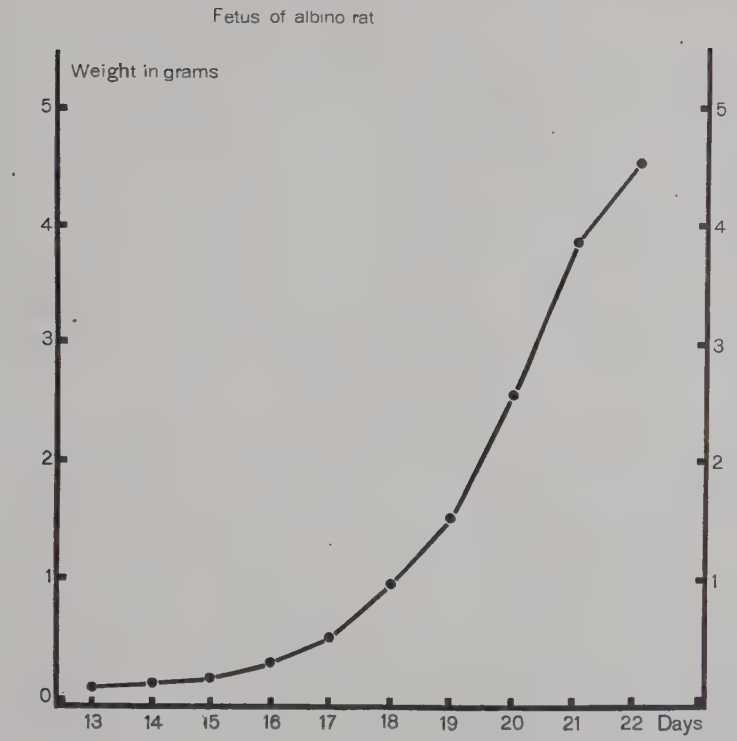

Chart 1 Showing the mean weights in grams of the fetuses of the albino rat at 24-hour intervals, from the 13th to the 22nd day of gestation, inclusive, based on the values given in table 2. The weights here given would be slightly increased if the mothers had all been fed on 'bread and milk,' and slightly diminished had the mothers all been fed on 'scrap.'

that of man we find the actual time ratio to be 1 to 13. Applying this ratio to the human records, the 13th day of gestation in the rat would correspond to the 169th day in man. If the weights in the two species—man and the rat—correspond during the gestation period, then at birth, 4.6 grams for the rat would represent 3250 grams for man. At the 13th day the rat fetus weighs 0.04 grams, so by proportion we would obtain a weight for the human fetus of 283 grams at 169 days. Speaking broadly, this seems to be too small a fetal weight for man (Jackson '09).

TABLE 3

Crown–rump length of fetus in millimeters; scrap diet only

SERIAL NO.	AGE IN DAYS	NUMBER IN LITTER	AVERAGE WEIGHT OF FETUS IN GRAMS	AVERAGE CROWN–RUMP LENGTH IN MM.	RANGE OF LENGTH IN MM.
42	14	8	0.093	9.5	9 –10
43	15	12	0.107	9.4	9 –10
38	15	8	0.218	12.1	12 –12.5
41	16	11	0.322	13.0	12.5–13
40	17	7	0.525	16.3	16 –17
36	18	9	0.947	19.1	18 –21
37	19	8	1.490	22.7	20.5–24
35	20	10	2.510	27.7	24 –32
34	21	9	4.070	36.7	35 –39
44	22	10	4.630	39.2	36 –41

It might be interpreted, however, as evidence for a still greater slowness of growth in the rat during the earlier period of gestation, but any attempt to follow the matter further must await better data on the weight of the human fetus at different ages.

The data contained in table 1 are sufficient to justify some further discussion of the characters and relations of the fetus during the period covered by the observations.

It is often desirable to have the data for fetal weight correlated with fetal length. Table 3 gives in a number of cases the crown-rump measurements *of the fresh fetus* after the membranes had been cleared away. The litters from scrap-fed mothers only have been used for this purpose.

A word of explanation touching the diets is here in place. In the course of these observations the general diet of the colony was changed. The earlier litters were from females fed on a diet in which bread and milk were the chief features—this is designated 'bread and milk,' while the later records were from females fed on a 'scrap' diet—i.e., table scraps from which materials known to be injurious to the rats had been excluded—this is designated as 'scrap.'

Two differences which are apparently related to the diet, appear, as can be seen from table 4, in which the data are arranged according to the diet of the mother.

In seven out of eight comparisons the litter number for the scrap diet is greater, while the average weight of the fetus is less for the scrap diet litters. Also in seven out of eight comparisons; the exceptional records are in parentheses. The lower average weights of the fetuses from the scrap-fed rats are about what we should expect to follow from the increase in the number in the litter (King '15) but the appearance of the larger number per litter in the scrap-fed series was an unexpected result. The distribution of the litter size (number of individuals) is a fairly symmetrical one and is shown in chart 2.

The mean value for the litter size is 8.8. Our laboratory records show a mean litter size of about 7.0 for the general

TABLE 4

Effect of diet on the number of fetuses in the litter and on the mean fetus weight

AGE, DAYS	DIET	NO. OF LITTERS	LITTER DESIGNATION	AVERAGE NO. IN LITTER	AVE. WT. OF FETUS, GRAMS
13	Bread and milk	3	(21) (22) (23)	9	0.041
	Scrap	1	(39)	(7)	0.037
14	Bread and milk	4	(20 (17) (14) (24)	8	0.117
	Scrap	1	(42)	14	0.093
15	Bread and milk	2	(7) (16)	8.5	0.174
	Scrap	2	(38) (43)	9.5	0.162
16	Bread and milk	4	(12) (25) (15) (5)	8	0.305
	Scrap	1	(41)	11	0.322
17	Bread and milk	2	(6) (18)	6.5	0.560
	Scrap	1	(40)	8	0.525
18	Bread and milk	2	(13) (4)	8.5	1.05
	Scrap	2	(36) (30)	13	0.95
19	Bread and milk	2	(2) (19)	6	1.59
	Scrap	2	(37) (31)	9	1.58
20	Bread and milk	1	(26)	8	2.95
	Scrap	2	(33) (35)	8.5	2.47
General average: Bread and milk				7.8	0.848
	Scrap			10.0	0.781

population of the colony (King and Stotsenburg '15). In the present case, however, it is to be remembered first, that we are dealing only with second litters, which tend to be large (King and Stotsenburg '15) and second, that there may be some tendency also for the fetuses to be more numerous than are the young actually born.

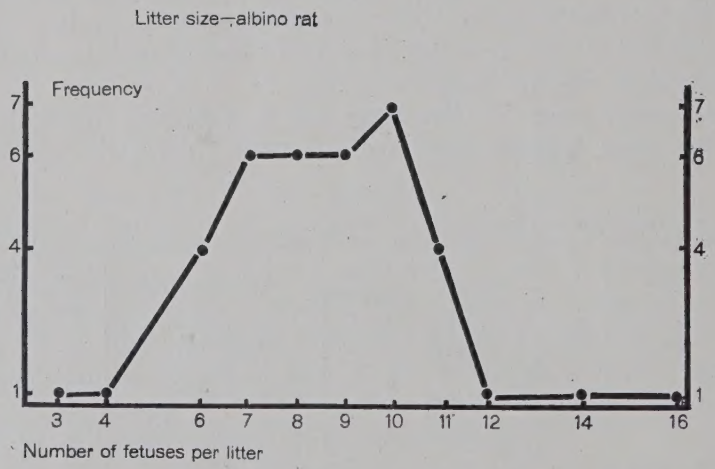

Chart 2 Showing the frequency, as indicated on the ordinate, of the litters containing from 3 to 16 fetuses, as indicated on the abscissa. The mean value is 8.8 fetuses per litter.

DISTRIBUTION OF THE FETUSES BETWEEN THE TWO HORNS OF THE UTERUS

This distribution was noted in the case of 20 litters and the details are given in table 5. *In toto* there were 90 fetuses in the right horn, 94 in the left. In two cases the right horn was sterile, and in four cases there was the same number of fetuses in each horn. If the comparison is made between the average weights of the fetuses in the two horns it is seen that in nine out of the fourteen possible comparisons the average weight of the fetus is greater in the horn containing the smaller number.

THE WEIGHT OF THE FETUS ACCORDING TO POSITION IN HORN

An examination of the fetal weights according to the position of the fetus in the horn has not revealed any correlation. At the same time, inspection of table 1 shows that marked variations in the weights of the fetuses in the same litter and even within the same horn may occur.

For the growth of the Albino from the beginning to the end of gestation, we already have the observations of Huber ('15) giving weight data for the first 3 days and 17 hours, so that there still remains to be filled the interval of about 10 days between the end of Huber's weight records, and the 13th day, which marks the beginning of the records here presented.

TABLE 5

Showing the number of fetuses in each horn of the uterus and their average weight

SERIAL NO.	AGE OF LITTER		NO. IN LITTER	LEFT HORN		RIGHT HORN	
	Days	Hours		No.	Weight	No.	Weight
21	13	2	10	3	0.041	7	0.041
22	13	2	10	7	0.043	3	0.042
23	13	2	10	6	0.044	4	0.048
39	13		8	3	0.039	5	0.036
17	14	2	7	7	0.121	0	
20	14	2	6	3	0.126	3	0.105
24	14	2	11	5	0.116	6	0.100
42	14		14	5	0.094	9	0.092
16	15		11	6	0.184	5	0.176
38	15		8	5	0.210	3	0.229
43	15		12	6	0.112	6	0.104
15	16		10	5	0.325	5	0.302
41	16		11	6	0.310	5	0.337
18	17		7	4	0.542	3	0.519
2	19		4	4	1.36	0	——
19	19		8	1	1.93	7	1.80
37	19		8	4	1.50	4	1.47
35	20		10	6	2.45	4	2.62
34	21		9	6	4.05	3	4.08
44	22		10	2	4.58	8	4.63
Total				94		90	

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